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ARTICLE

Ecosystem classification and mapping of the Laurentian Great Lakes

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Abstract: Owing to the enormity and complexity of the Laurentian Great Lakes, an ecosystem classification is needed to better understand, protect, and manage this largest freshwater ecosystem in the world. Using a combination of statistical analyses, published knowledge, and expert opinion, we identified key driving variables and their ecologically relevant thresholds and delineated and mapped aquatic systems for the entire Great Lakes. We identified and mapped 77 aquatic ecological units (AEUs) that depict unique combinations of depth, thermal regime, hydraulic, and landscape classifiers. Those 77 AEU types were distributed across 1997 polygons (patches) ranging from 1 to >48 000 km² in area and were most diverse in the nearshore (35 types), followed by the coastal margin (26), and then the offshore (16). Our classification and mapping of ecological units captures gradients that characterize types of aquatic systems in the Great Lakes and provides a geospatial accounting framework for resource inventory, status and trend assessment; research for ecosystem questions; and management and policy-making.

Résumé : En raison de l'énormité et de la complexité des Grands Lacs laurentiens, une classification des écosystèmes est nécessaire pour mieux comprendre, protéger et gérer ce plus grand écosystème d'eau douce du monde. En utilisant une combinaison d'analyses statistiques, de connaissances publiées et d'opinions de spécialistes, nous avons cerné des variables clés et leurs seuils importants sur le plan écologique, et délimité et cartographié les systèmes aquatiques pour l'entièreté des Grands Lacs. Nous avons cerné et cartographié 77 unités écologiques aquatiques (UEA) qui représentent les différentes combinaisons de profondeur, de régime thermique et de variables hydrauliques et du paysage importantes pour la classification. Ces 77 types d'UEA sont répartis sur 1997 polygones (parcelles) de superficies allant de 1 à >48 000 km², la région sublittorale en présentant la plus grande diversité (35 types), suivie des bandes côtières (26), puis de la zone extracôtière (16). La classification et la cartographie des unités écologiques font ressortir les gradients qui caractérisent les types de systèmes aquatiques dans les Grands Lacs et fournissent un cadre géospatial de référence pour l'inventaire des ressources, l'évaluation des statuts et tendances, la recherche sur des questions touchant aux écosystèmes et la gestion et l'élaboration de politiques. [Traduit par la Rédaction]

Introduction

Ecosystems are composed of complex interactions of biotic and abiotic components that are linked through the physicochemical environment and energy flows, controlled by both external and internal factors occurring at multiple spatial and temporal scales (Jensen et al. 2001; Klijn and Haes 1994). Ecosystem complexity presents challenges for research, management, and assessment, because the wide range of ecological conditions at local scales limits our ability to understand and predict variation within smaller-scale ecosystems components without geographic context at the macroscale (Bailey 2014; Wehrly et al. 2013). The inherent complexity of an ecosystem can be simplified by compartmentalizing or classifying key drivers of ecological patterns and processes that capture variability across space and time into relatively homogeneous units. The types and inherent linkages of such units provide an effective way for describing local conditions and broader ecological patterns (Klijn and Haes 1994; Wu and David 2002; Higgins et al. 2005; Kurtz et al. 2006; Guarinello et al. 2010). Classifications simplify and organize multifaceted systems, provide a framework for organizing our general knowledge of the complexities of natural systems, and provide scientists and managers with a structure for managing resources, prioritizing research, and identifying conservation needs across ecotypes (Omernik 1987; Kurtz et al. 2006; McKenna and Castiglione 2010). Broadscale classifications of types of soils or land cover, for example, across the US have been used extensively for inventory, monitoring, assessment, and planning (Cowardin et al. 1979; Riseng et al. 2006; Danz et al. 2007; Elrashidi et al. 2014).

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The Laurentian Great Lakes are the largest freshwater ecosystem in the world, with a complicated geology, bathymetry, and climate that creates complex patterns of temperature, mechanical energy, water quality, and biological assemblages within and among the lakes (Wehrly et al. 2013). As with other large, complex ecosystems, a universally applicable classification system that helps organize and simplify this complexity would substantially advance monitoring, assessment, management, and research of the Great Lakes.

There are many ways to classify ecosystems and many dimensions to consider when comparing across different classification systems (e.g., Herdendorf et al. 1992; Jensen et al. 2001; Bailey 2009). However, we believe there are four key dimensions that are particularly useful for comparing among classification systems and more clearly distinguishing ours from other existing classifications. These four dimensions include (*i*) classification method (e.g., top-down versus bottom-up), (*ii*) ecological attributes (e.g., physical versus biological and structure versus function), (*iii*) spatiotemporal scale(s), and (*iv*) level of development (i.e., conceptual versus mapped). For our classification system, we used a top-down approach that focused on physical drivers operating at large spatial and long temporal scales across the entire Great Lakes and took into consideration both ecosystem structure and function. We also took our classification beyond a conceptual framework by mapping these drivers within a GIS framework so that the resulting classification could be used for planning, management, and research.

To date, classifications of the Great Lakes ecosystems have been conceptual (Busch and Sly 1992; Higgins et al. 2005) or limited to specific areas or features (e.g., shoreline; coastal wetlands) or specific biota (Table 1; Busch and Lary 1996; Keough et al. 1999; Albert et al. 2005; Johnson et al. 2007). Busch and Sly (1992) outlined a conceptual hierarchical classification for the Great Lakes based on energy-related variables (e.g., wind, temperature, and light) and lake morphometric descriptors (e.g., depth and bottom configuration). This conceptual classification hierarchy subdivided a lake (system) into two zones: open water and nearshore (subsystem), and further divided subsystems based on circulatory basin and shoreline complexity, substrate, plant material, and water column properties. This classification concept was applied to Lake Ontario to assess habitat impairments based on primarily depth, substrate, and plant cover (Busch and Lary 1996). Data needed to implement this classification were incomplete, which limited the ability to map classes and apply to other lakes. Johnson et al. (2007) developed a dynamic classification based on multiple integrated geospatial data layers that combined information on physical, chemical, and biological attributes for the Lake Erie basin from watersheds to open water habitats. Enhanced geospatial resolution and increased availability of biotic and habitat-related data would provide the opportunity to consolidate and improve the existing classification systems for the entire Great Lakes basin.

In 2012, US federal agencies (National Oceanic and Atmospheric Administration (NOAA), NatureServe, United States Environmental Protection Agency (US EPA), and United States Geological Survey (USGS)) published a comprehensive US federal standard and lexicon for classifying and describing marine ecosystems from tidal estuaries to deep ocean waters (Coastal and Marine Ecological Classification (CMECS); FGDC 2012), which has not yet been applied to the Great Lakes. The CMECS classification system is a hierarchical organization of biogeographic and aquatic settings of water column, geoform, substrate, and biota, which can be combined depending on user-specified applications. However, because classification levels are co-mingled and described units are not georeferenced, applying this system to map ecosystem classes is difficult. Great Lakes coastal wetlands have been classified into hydrogeomorphic types using key variables that describe hydrologic, geomorphic, exposure, and vegetative characteristics of coastal wetlands, which has provided a conceptual framework for monitoring and assessment (Keough et al. 1999; Albert et al. 2005).

Several fish-based habitat classifications have been developed for an individual Great Lake based on species–habitat relationships (Table 1). McKenna and Castiglione (2010) developed a fish habitat classification for the western basin of Lake Erie based on circulation patterns, temperature, and shoreline features. This system has been further applied for the entire Great Lakes region (McKenna and Castiglione 2017). Chu et al. (2014) developed a nearshore fish habitat classification for the nearshore zone of Lake Ontario using lake and watershed characteristics that were associated with fish community composition. Rutherford and Geddes (2007) developed a Great Lakes basin-wide classification of fish habitat for fisheries management using bathymetry, temperature, substrate (some lakes), proximity to tributaries, and circulation patterns. These studies classified and mapped habitat units for Great Lakes but were limited to species-specific habitat relationships and therefore have limited application to other biota or ecological processes.

Development of a systematic classification and mapping tool for the aquatic portion of the Great Lakes requires a basin-wide spatial framework, linked to harmonized ecological data across the US and Canadian portions of the basin that facilitates aggregation of information into homogeneous units. The recently developed Great Lakes Aquatic Habitat Framework (GLAHF) provides the needed hierarchical spatial units and a suite of physicochemical and biological variables that are spatially referenced to enable a GIS-based approach for mapping and visualizing an aquatic ecosystem classification for the entire Great Lakes basin (Wang et al. 2015). The GLAHF spatial framework consists of spatial units (30 m raster cells) that are attributed with data and nested within ecological zones, lake sub-basins, lake basins, and the entire Great Lakes basin. The GLAHF's spatial classification framework delineates five ecological zones that cover all the riparian and aquatic areas of the Great Lakes basin: catchments linked to coastal areas by drainage points, coastal terrestrial areas, coastal margin areas, nearshore areas, and offshore areas.

In this study, we developed a process to classify aquatic units based on ecosystem attributes using the GLAHF spatial framework and associated ecological data. We used information from the literature and input from experts of Great Lakes ecology to identify ecosystem drivers, variables, and thresholds to map ecosystem units and types. Our goal was to classify and map aquatic ecological units (AEUs) that captured broadscale dominant physical processes that structure Great Lakes ecosystems. Our objectives were to (*i*) classify and map AEUs across the entire Great Lakes basin using consistent basin-wide data that would be useful for multiple purposes and applied at a variety of spatial scales; (*ii*) build upon existing classifications and expert knowledge to achieve a "next-generation" ecosystem classification and mapping of the entire Great Lakes; (*iii*) use the existing GLAHF spatial framework and database as the foundation for mapping the ecological units; and (*iv*) make the resulting geospatial mapping products of the classification publicly available. Our classification and mapping is novel in that it is the first effort to account for all of these factors for the entire Great Lakes Basin.

Methods

Our classification approach had four major steps: (1) identify key controlling variables; (2) reduce and select variables; (3) identify thresholds for selected variables; and (4) aggregate variables and map units. The critical first step in the classification process involved identifying a set of the key controlling factors that influence ecosystem patterns at multiple spatial scales (Klijn and Haes 1994). Based on literature review and expert opinion, we identified four controlling factors that are known to influence the major physicochemical and biological characteristics of the Great

Table 1. Summary of published classification systems for the Great Lakes.

Project–classification	Authors	Goals	Extent	Scale	Input variables	End product
The development of an aquatic habitat classification system for lakes	Busch and Sly 1992	Hierarchical classification systems including system, subsystem, division, subdivision, and class levels	Aquatic ecosystems	Not defined	Depth, circulation, and morphologic shoreline features further defined by water column, substrate, and plant material characteristics	Conceptual Hierarchical Aquatic Habitat Classification system
Assessment of habitat impairments impacting the aquatic resources of Lake Ontario	Busch and Lary 1995	Follow Busch and Sly (1992) Aquatic Habitat Classification approach to evaluate impairment of habitat types	Lake Ontario	Not defined	See Busch and Sly 1992	88 habitat types evaluated for degree of impairment
Hydrogeomorphic factors and ecosystem responses in coastal wetlands of the Great Lakes	Keough et al. 1999	Characterize coastal wetlands along a hydrogeomorphic continuum to provide a framework for restoration and management	Great Lakes wetlands	Not defined	Hydrogeomorphic types further defined by site-specific characteristics such as nutrients, sediments, and shoreline features	Classification framework for organizing Great Lakes wetlands
Hydrogeomorphic classification for Great Lakes coastal wetlands	Albert et al. 2005	Apply a hierarchical hydrogeomorphic classification system that can be used to consistently characterize and potentially map all of the coastal wetlands of the Great Lakes	Great Lakes wetlands	Not defined	Classified first by hydrogeomorphic type (lacustrine, riverine, or barrier-protected), then by geomorphic features and processes	17 different wetland classes defined first by hydrologic character and then by geomorphic types and modifiers
A freshwater classification approach for biodiversity conservation planning	Higgins et al. 2005	Spatially hierarchical approach to classifying aquatic ecosystems based on expert input to select variables and classes	Applied in North, South, and Central America	100 000 to 100 km²	Zoogeographic (user-defined regional zoogeography); ecological drainage unit (e.g., landform, geology); aquatic ecological system (e.g., hydrologic, temperature regime); macrohabitat (e.g., position, complexity)	Classification approach and three cases studies demonstrating application; variable depending on case study
Integrated habitat classification and map of the Lake Erie basin	Johnson et al. 2007	An integrated habitat classification and map for the Lake Erie basin to assess the status and trends in the quantity and quality of fish and wildlife habitats	Lake Erie	Not defined	Numerous physical (energy and structure) and chemical (geology and anthropogenic) attributes that regulate habitat	Six natural land and water habitat zones based on landscape features and dominant physical processes; hydrogeomorphic classification of coastal wetlands
Ecological classification of nearshore and open water fish habitats in the Great Lakes	Rutherford and Geddes 2007	Fish-based ecological classifications of nearshore and offshore habitats in the Great Lakes	Great Lakes	3 km grids	Bathymetry, slope, summer temperature, substrate, proximity to river mouth, and circulation patterns	Two nearshore and three to four offshore units classified separately and by lake
Hierarchical multiscale classification of nearshore aquatic habitats of the Great Lakes: western Lake Erie	McKenna and Castiglione 2010	Describe the C-Gap hydrospatial framework and demonstrate a habitat classification system using fish	Western Lake Erie	90 m² cells	Lake shoreline variables, size–distance to nearest tributary, lake bathymetry, predicted submerged aquatic vegetation, temperature	32 habitat types nested in 11 coastal or open water zones (and one deepwater zone)
Coastal and Marine Ecological Classification Standard (CMECS)	Federal Geographic Data Committee 2012	Describe the major aquatic settings within the coastal and marine environment	US coastal marine areas	Not defined	Water column; surface geology; benthic biotic, subbenthic, and geoform components	Map overlays; determined by user objectives
An ecological classification for the nearshore zone of Lake Ontario	Chu et al. 2014	Ecologically based habitat classification of fish habitat for the nearshore of Lake Ontario	Canadian nearshore areas of Lake Ontario	1 km shoreline reaches	Average effective fetch, elevation profile, development, and dense coniferous forest	Ecological classification of nearshore reaches

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Lakes (Wichert et al. 2004; Johnson et al. 2007; McKenna and Castiglione 2010; FGDC 2012): bathymetry, thermal regime, mechanical or hydraulic energy, and connection to tributaries and watersheds.

Water depth is widely recognized as an organizing factor in lentic ecology that separates habitat types and is commonly used to stratify monitoring studies (Rawson 1950; Stevens and Olsen 2004; Sierszen et al. 2014). Wetzel (2001) identified morphometry (including depth) as an important factor for characterizing physicochemical and biological characteristics of inland lakes. Depth is associated with thermal stratification and the limits of light penetration and is a key factor in describing general patterns of energy and nutrient processing on average (Rawson 1950; Herdendorf et al. 1992). Productivity gradients across the Great Lakes that are driven by climate, land form, and patterns of anthropogenic disturbances (Brazner et al. 2007; Danz et al. 2007) also commonly vary with depth. Shallow coastal and nearshore waters typically have increased nutrient inputs from tributary watersheds, which can result in increased productivity (Yurista et al. 2012). In contrast, deeper offshore waters have less material inputs from tributary watersheds (Yurista et al. 2015, 2016), which can result in reduced productivity, although episodic storm events can enhance nearshore–offshore nutrient transport (Eadie et al. 2002). The distribution of many aquatic organisms exhibit depth-related patterns. For example, densities of *Diporeia*, a benthic keystone genus in the Great Lakes, varied significantly with depth and were most common in a zone (30–125 m) that represented only one-quarter of total benthic habitat in Lake Superior (Auer et al. 2013). Over 80% of Great Lakes fishes require shallow water for spawning (over a variety of substrates), while others require deep-water reefs for spawning, which illustrates the importance of depth as an integrating and organizing force for Great Lakes aquatic habitats (Lane et al. 1996).

Thermal regime is a key variable influencing the metabolism, growth, life histories, distribution, and abundance of aquatic taxa from phytoplankton to fish (Magnuson et al. 1997; Brown et al. 2004). In this paper, we use thermal regime to represent the spatial and temporal variability in water temperature (Poole et al. 2004). The thermal regime in the Great Lakes is determined by regional climatic patterns interacting with lake morphology, stratification pattern, and upwellings (Bennett 1978). It also influences physical factors such as ice cover extent and duration (Mason et al. 2016) and the vertical and horizontal distribution of currents (Bennett 1978). Fetzer et al. (2017) found that spatial differences in nearshore fish assemblages in Lake Michigan and Lake Huron were, in part, related to differences in thermal regime among sites. Wehrly et al. (2012) found that differences in thermal regime among lakes was an important predictor of fish assemblage structure in inland lakes of Michigan. Similarly, Mehner et al. (2007) concluded that differences in thermal regime among lakes was an important factor explaining latitudinal differences in fish assemblages in European lakes.

Mechanical energy here mainly represents the energy transferred from wind to water resulting in waves, longshore currents, gyres, seiches, and upwelling. Water motion in the form of waves and circulation influences erosion, transportation and deposition of sediments, and transport and distribution of nutrients and material from tributaries and within the water column (Herdendorf et al. 1992). Mechanical energy influences the distribution of fish and other organisms and is a primary hydrogeomorphic factor explaining the formation of some coastal wetland types (Keough et al. 1999). Webb et al. (2008) showed that turbulent water movement in coastal areas affected fish species distribution and densities and suggested that wave energy would be a useful variable for ecosystem classification. In high energy shallow areas, wave exposure can result in unstable substrates, whereas deeper areas of the lakes are exposed to lower energy transport and circulation currents (Kalff 2002). Glyshaw et al. (2015) found different benthic communities as depth increased from 15 to 90 m and identified wave and transport energy as one factor that structured the benthos.

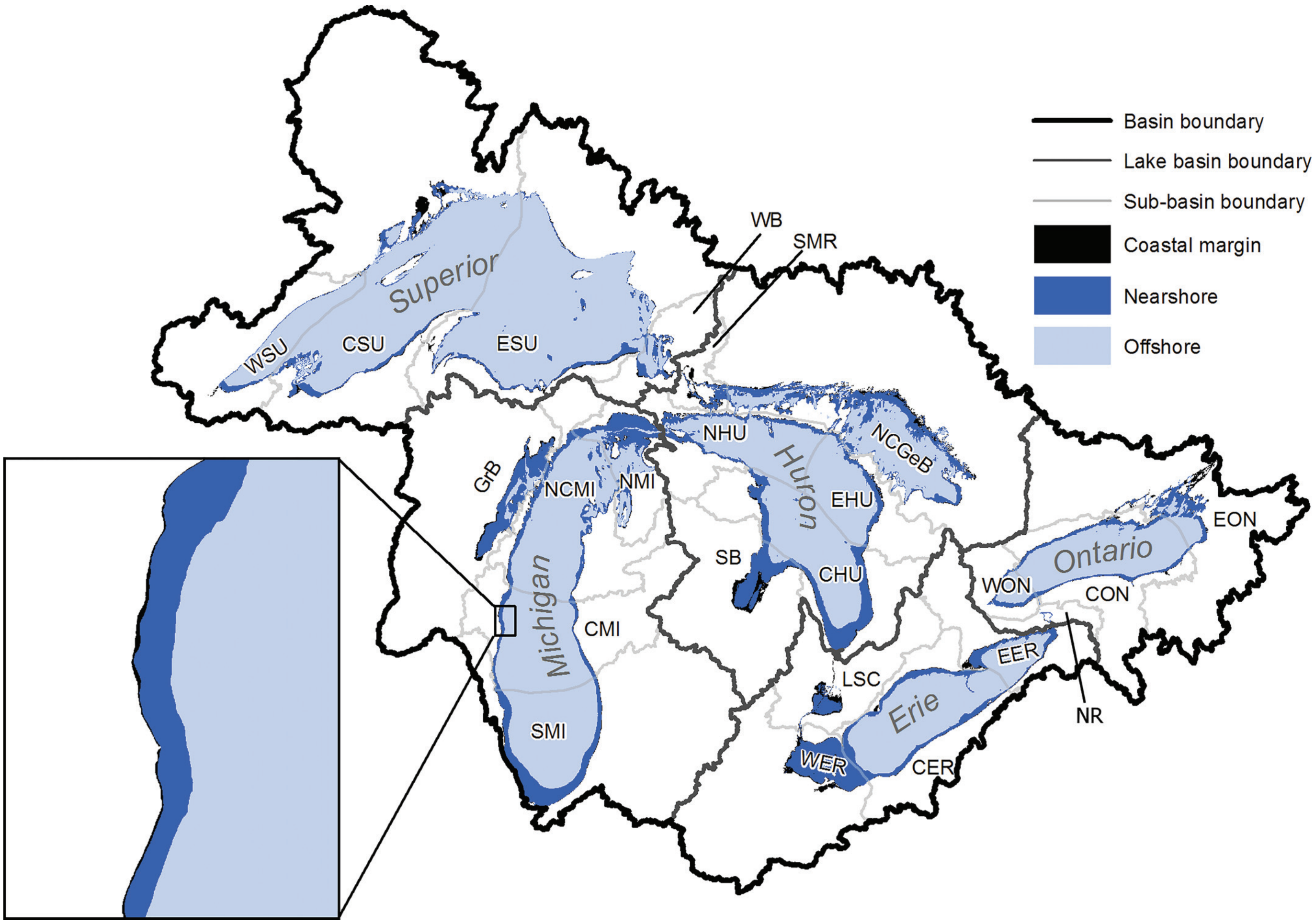
Tributaries influence ecological conditions in nearshore habitats via inputs of nutrients, sediments, and biological exchange (Herdendorf et al. 1992). Materials delivered from tributary watersheds tend to be entrained in the coastal and nearshore regions due to lake hydrodynamics, although highly diluted tributary runoff eventually mixes with offshore waters (Csanady 1970; Yurista et al. 2015). The entrainment of tributary runoff in the nearshore results in more variable turbidity and water chemistry, compared with more uniform and dilute offshore waters (Yurista et al. 2016). Flux of sediments and nutrients from tributaries influences nearshore water chemistry, productivity, and benthic and fish communities (Makarewicz et al. 2012).

Variable reduction and selection

The next step in the classification process involved selecting a subset of variables to represent each of the four controlling factors. From the GLAHF database, we identified variables that could be used to describe the influences of depth, thermal regime, mechanical energy, and tributary inputs to the Great Lakes, 26 in the offshore and 54 in the nearshore (Wang et al. 2015; Table A1). For example, there were 19 variables to describe mechanical energy in the GLAHF database. To reduce the number of variables, we used correlation and ordination statistical analyses, published relationships, and expert knowledge to select four variables that best represent the mechanical energy factor for classifying and mapping of Great Lakes ecosystems.

The GLAHF spatial framework has about 230 million basic spatial units (at the 30 m cell resolution). To reduce computational and time constraints for statistical analyses, we analyzed data from a randomly selected subset of units stratified by lake and then by ecological zone (Fig. 1) so that each zone and lake were equally represented in the analyses (N = 20 000). We first used simple pairwise correlation analysis of all variable combinations to identify pairs of highly correlated ($r > 0.8$) variables within each controlling factor. From each highly correlated pair, we selected variables that best represented broad spatial and temporal scales of variation (e.g., cumulative temperature distributions versus local temperature variation). Spring and summer temperatures were highly correlated, so we selected summer temperatures to reflect known ecological limits during summer stratification. We then used principal components analysis (PCA) to identify the linear combinations of variables within each controlling factor that best explained variation in each zone and selected variables that accounted for the most weight (positive or negative) on the first two axes. To select variables that accounted for the most weight, variable weights were plotted in rank order and visually examined to determine the first substantial decrease in weight. Variables were retained if they were above this predetermined threshold, generally between 0.7 and 0.8. Lastly, we related the retained variables to biological community measures using a combination of correlation and forward selection canonical correspondence analysis (CCA; ter Braak and Smilauer 2002; McKenna and Castiglione 2010) to ensure that the selected physical variables were relevant to a suite of biological communities in the Great Lakes. Similar biological data were not available for all five Great Lakes, depth zones, or time periods, so we used the best available data in GLAHF to identify variables that would collectively relate to multiple biological communities of the Great Lakes (Wang et al. 2015). We used correlation to assess relationships among retained environmental variables with the following biological variables: spring and summer epilimnetic chlorophyll *a* data averaged from 2003 to 2005 (Lakes Ontario, Erie, Huron, and Superior; nearshore N = 69, offshore N = 59); and benthic taxa richness in the offshore zone for all lakes primarily in the offshore zone (N = 53) summarized over 2006–2011 (benthos data were not

Fig. 1. Lakes, lake sub-basins and aquatic zones (revised from Wang et al. 2015): Lake Erie (CER — central Lake Erie, EER — eastern Lake Erie, LSC — Lake St. Clair, WER — western Lake Erie); Lake Huron (CHU — central Lake Huron, EHU — eastern Lake Huron, NCGeB — North Channel and Georgian Bay, NHU — northern Lake Huron, SB — Saginaw Bay, SMR — St. Marys River); Lake Michigan (CMI — central Lake Michigan, GrB — Green Bay, NCMI — north-central Lake Michigan, NMI — northern Lake Michigan, SMI — southern Lake Michigan); Lake Ontario (CON — central Lake Ontario, EON — eastern Lake Ontario, NR — Niagara River, WON — western Lake Ontario); and Lake Superior (CSU — central Lake Superior, ESU — eastern Lake Superior, WB — Whitefish Bay, WSU — western Lake Superior). Aquatic zones are coastal margin, nearshore, and offshore (see inset). [Colour online.]



available for the nearshore zone). We used CCA to evaluate the relationships of the retained environmental variables with benthos and fish assemblage metrics (Lake Ontario, all zones, N = 3531; J. McKenna, unpublished data) and retained the CCA variables that best explained variance for each zone; for fish we assumed that relationships found using the Lake Ontario data were applicable across all five lakes. We then identified three to five least-correlated variables to represent each controlling factor for further examination.

Selection of the final variables used for classification and mapping reflected an objective reduction process, as well as consideration by experts, ecological knowledge from studies relating habitat conditions to biological communities, and findings from previous Great Lakes classifications (Johnson et al. 2007; McKenna and Castiglione 2010; Chu et al. 2014). The final variables selected for classifying AEUs included depth (bathymetry), cumulative degree-days (CDD) for epilimnetic waters (thermal regime), nearshore and offshore circulation patterns and coastal and nearshore exposure (mechanical energy), and tributary influence on nearshore waters. For each variable, thresholds were identified to create a limited number of classes that represented observed organizing patterns for large lake ecosystems. When possible, existing empirically determined thresholds were used to create discreet classes; if empirical studies were not available, natural statistical breaks (Jenks natural breaks classification method) were used, recognizing that statistical breaks may or may not be biologically relevant. The final classification and map of unique AEUs represents a combination of four variables and their associated thresholds into a four-level ecological classification that is comparable to other three- or four-level classification frameworks developed for freshwater and marine systems (Higgins et al. 2005; Albert et al. 2005; FGDC 2012). Descriptions of the variables and criteria used for the lake-wide classification (Table 2) are described below.

AEU variables and thresholds

Bathymetry

We identified five bathymetric thresholds that were related to littoral energy, aquatic vegetation extent, stratification limits, and light extinction (Table 2; Fig. 2). First we defined the nearshore as a well-mixed zone, distinct from the stratified offshore and where longshore currents dominate, and is often thought to be the approximate depth limit of tributary influence (Yurista et al. 2012, 2016; Kelly et al. 2015; Scharold et al. 2015; Wang et al. 2015). We defined the extent of the nearshore zone as <30 m depth

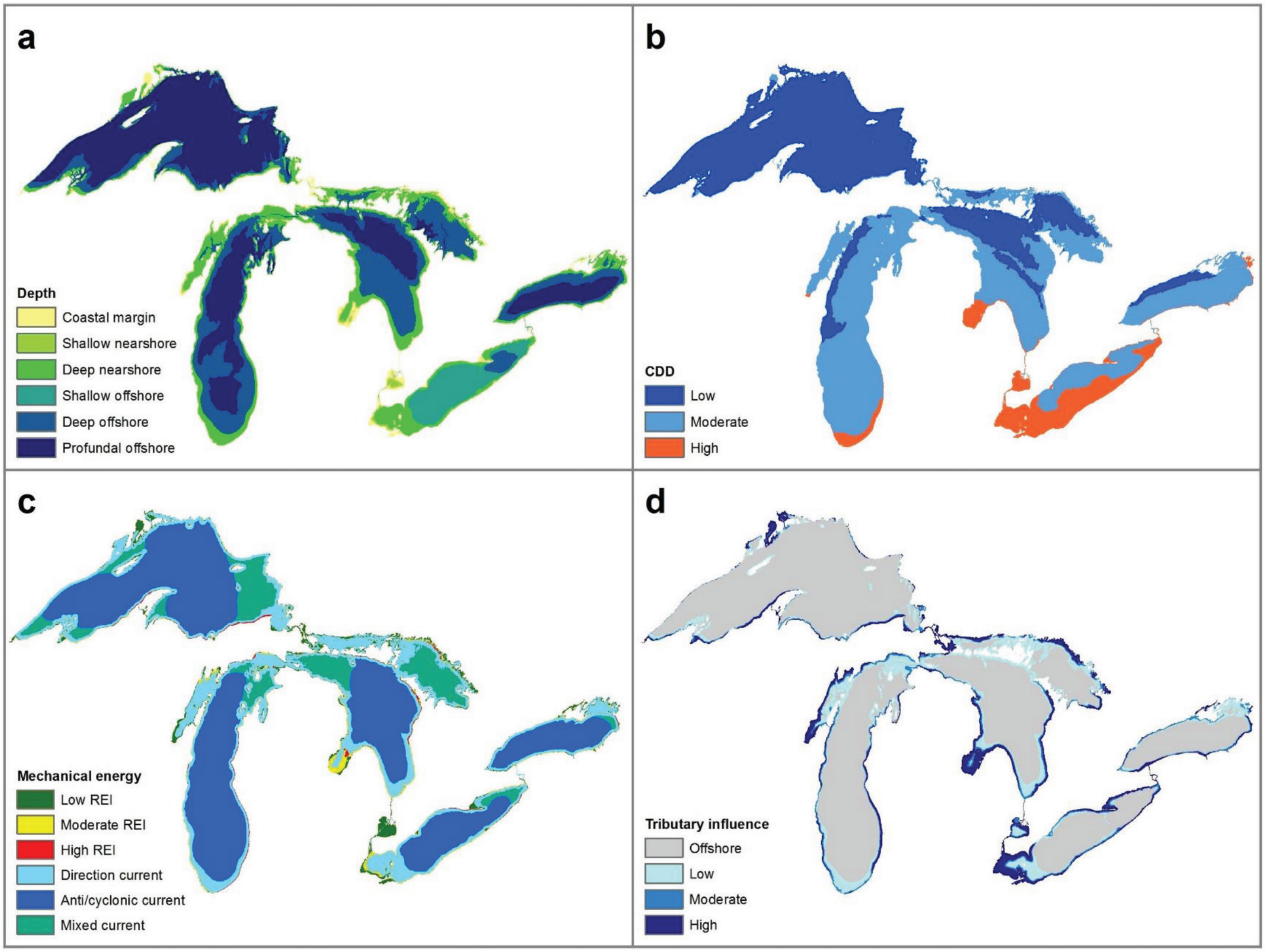
Table 2. Selected classification variables, criteria thresholds, threshold rationale, and supporting documentation for criteria thresholds.

Driver (variable(s))	Class	Description	Threshold	Rationale	Source
Depth (bathymetry)	1	Coastal margin	High water mark to 3 m	Wave splash zone; coastal margin–nearshore boundary	Rao and Schwab 2007
	2	Shallow nearshore	3–5 m	Maximum depth at which submergent vegetation dominates	Kalff 2002; McKenna and Castiglione 2010
	3	Deep nearshore	5–30 m (15 m)	Nearshore–offshore boundary; depth contour extent of tributary influence; thermocline boundary; 15 m in Lake Erie	Yurista et al. 2012; Kelly et al. 2015; Mackey 2012
	4	Shallow offshore	15–30 m	Lake Erie only, shallow zone with characteristics of offshore (circulation, stratification)	Kelly et al. 2015; Wang et al. 2015; Yurista et al. 2016
	5	Deep offshore	30–100 m	Stratification depth and >1% light penetration	Kalff 2002
	6	Profundal offshore	>100 m	<1% light penetration	Wetzel 2001
Thermal energy (epilimnetic cumulative degree-days (CDD))	1	Low	<3000 degree-days	Dominated by cold-water fish species	Wehrly et al. 2013; Neuheimer and Taggart 2006
	2	Moderate	3000–3900 degree-days		
	3	High	>3900 degree-days	Dominated by warm-water fish species	
Mechanical energy (relative exposure index (REI) and circulation patterns)	1	Low REI	<125 000	Protected shorelines, embayments	Keddy 1982; Meadows et al. 2005 (link wave energy, currents, and shoreline processes)
	2	Moderate REI	125 000–300 000	Areas of moderate wave energy (Lake Erie)	
	3	High REI	>300 000	Areas of high wave energy (Lake Erie)	
	4	Directional current			Beletsky et al. 1999; Rao and Schawb 2007; Kelly et al. 2015
	5	Cyclonic circulation			Bennington et al. 2010; Sheng and Rao 2006; Prakash et al. 2007; Schwab et al. 2009; Beletsky et al. 2013
	6	Mixed circulation			
Tributary influence	0	None		Offshore zone	
	1	Low	<30 km² watershed area	Nearshore zone	First- and second-order streams
	2	Moderate	30–250 km² watershed area		Allan et al. 2013
	3	High	>250 km² watershed area		Allan et al. 2013

contour in all Great Lakes, except Lake Erie where we used the greater of a 15 m depth contour or 5 km from shore to capture the well-mixed zone. A 30 m depth has been commonly accepted as the maximum average depth where the thermocline meets the lake bottom (Mackey 2009). Also, longshore currents that mix nearshore waters typically extend to 30 m, or between 3 and 5 km offshore (C. Troy, Purdue University, personal communication, 2015), where the deeper alternate deposition pathways often begins in large lakes (Kalff 2002). For Lake Erie, where most of the lake is less than 30 m, the nearshore has been defined several ways, including with a 15 m depth threshold (Mackey 2012) or a combination of depth and distance from shore (Kelly et al. 2015; Wang et al. 2015; Yurista et al. 2016).

Within the nearshore zone, wave energy and turbulence are the major factors structuring coastal ecosystems for the "coastal margin" zone (0–3 m depth zone). Smaller-sized substrate is easily mobilized through wave disturbance (wave splash zone) and transported by waves and nearshore currents, and fine sediments could be resuspended during large storm events (Rao and Schwab 2007). We also defined a 3–5 m "shallow nearshore" depth zone to capture the minimum extent of rooted submerged macrophytes. This 3–5 m zone extends to the approximate total depth range of wave influence but does not include the more turbulent wave-splash zone (Kalff 2002). These two zones could be used in finer-scale studies to denote the complex energy zones of the nearshore. We defined a "deep nearshore" zone between 5 and 30 m (or 15 m in Lake Erie) that extends to the typical maximum depth of the thermocline and longshore current mixing as described above. A zone unique to Lake Erie, the "shallow offshore", was defined as occurring between 15 and 30 m due to a difference in currents (longshore currents are not typical in Lake Erie) and variation in the extent and depth of annual summer stratification (Rucinski et al. 2010). In the offshore (>30 m depth) we defined two zones: "deep" and "profundal". The "deep offshore" zone was de-

Fig. 2. Variables associated with the four classification factors and their threshold criteria used to define the aquatic ecological units: (*a*) depth, (*b*) cumulative degree-days (CDD), (*c*) mechanical energy (REI, relative exposure index and circulation patterns), and (*d*) tributary influence.



fined as the region 30–100 m in depth. The 100 m depth represents 1% limit of light penetration (Wetzel 2001) and where the photosynthesis to respiration ratio is <1. Depths greater than 100 m were classified as the "profundal offshore" zone. At any one location in the Great Lakes, these depth categories may not accurately describe exact local conditions due to temporal variation in water levels, temperature profiles, and currents, but the thresholds identified here represent general depth categories that limit conditions for the suite of biological communities.

Bathymetric data were obtained from the NOAA National Centers for Environmental Information (NCEI, formerly National Geophysical Data Center). The original raster in 3-second resolution (approximately 90 m) was standardized to the GLAHF framework grid, and anomalous depth values incongruous with depth data from the NOAA Nautical Chart 14968 were removed. The 0 m depth was defined using the jurisdictional ordinary high water mark (USACE 1985), which was integrated with the high-resolution shoreline, including island polygons greater than 10 ha (Forsyth et al. 2016) and enforced as the land–water boundary. The final depth zones were smoothed by filling in any small pockets of shallow or deep areas within a larger continuous depth zone (Kelly et al. 2015). This step removed some fine-scale bathymetric variability but was needed to eliminate numerous small, incidental polygons. Removal of these polygons affected less than 2% of the total surface area of the Great Lakes and greatly simplified the classification. To maintain the depth variability that represents complexity in bottom surfaces, an additional layer was created to describe (*i*) deep areas within shallow zones and (*ii*) shallow areas within deep zones that could be used as an overlay for ecosystem mapping.

Temperature

CDD is an index of the thermal energy experienced by organisms over a given period of time (Venturelli et al. 2010). Spatial and temporal variation in CDD is useful for explaining differences in development, growth, habitat suitability, and assemblage structure of fishes (Venturelli et al. 2010; Wehrly et al. 2012; Hansen et al. 2017). CDD was calculated as the sum of mean daily epilimnetic water temperatures during ice-free days (above a base of 0 °C) from 1 January through 31 December and averaged from 2006 to 2012 to capture a range of variation in annual temperatures. We chose to summarize CDD for the epilimnion because the majority of fish species are found in the epilimnion and because, in contrast with hypolimnetic temperatures that remain a consistent 4 °C year round, epilimnetic temperatures exhibit large spatial and temporal gradients that are important in structuring ecological differences within and among lakes. In the nearshore and offshore zones (>5 m), modeled vertical water temperature was

Table 3. Distribution of the size of aquatic ecological unit (AEU) patches in different depth zones.

	Polygon area (km²)								
Depth zone	<1	1–10	10–25	25–50	50–100	100–1000	>1000	Subtotal	Max. area
<3 m	0	669	92	32	21	11	0	825	586
3–5 m	0	395	58	24	8	5	0	490	262
5–30 m (no ER)	0	206	79	62	39	67	8	461	2 653
5–15 m (ER only)	0	14	2	0	4	8	3	31	2 012
15–30 m (ER only)	0	0	0	0	0	2	2	4	7 076
30–100 m	0	0	31	15	21	50	17	134	12 994
>100 m	0	0	6	15	5	18	8	52	47 714
Total	0	1 284	268	148	98	161	38	1 997	

Note: ER indicates Lake Erie.

used to calculate a mean daily temperature for the depth range of 0–20 m, representing average epilimnetic temperatures (http://www.glerl.noaa.gov/res/glcfs/). In shallow nearshore zones (<5 m), where modeled temperatures are relatively coarse-grained, mean water temperature was calculated from surface water satellite estimates (http://coastwatch.glerl.noaa.gov/). The resultant CDD estimates from the shallow nearshore, the deep nearshore, and offshore zones were combined into a composite data layer.

We classified CDD into low, moderate, and high categories (Table 2; Fig. 2). Wehrly et al. (2012) studied over 200 inland lakes in Michigan, USA, and reported that lakes having high degree-days were dominated by warm-water fishes, while lakes having moderate degree-days were dominated by cool- and cold-water fishes. We used a threshold of 3900 degree-days to delimit the break between medium and high categories (Wehrly et al. 2012). The CDD in Michigan inland lakes do not span the lower range of CDD observed in the Great Lakes. To identify a lower threshold, we overlaid cool- and cold-water fish distribution maps (Bailey et al. 2004) on a map of CDD and identified a substantial shift to predominately cold-water fishes at 3000 degree-days.

Mechanical energy

We identified two variables to represent mechanical energy associated with coastal and offshore water motion: a relative exposure index for the coastal margin and shallow nearshore zones (<5 m) that summarized wave energy; and a generalization of circulation patterns for deep nearshore and deep and profundal offshore areas (Table 2; Fig. 2). The relative exposure index (REI) is a wind speed, direction, and frequency weighted measure of effective fetch (Keddy 1982). Fetch is the distance across the lake that wind blows typically in the predominant direction and is related to the range of wave height and periodicity characteristics at different locations around the coastal areas of the Great Lakes (Minns and Wichert 2005). Fetch has been commonly used to characterize the exposure of coastal areas to winds and as a predictor of coastal wetlands types (Keough et al. 1999; Cooper et al. 2014); nearshore macrophyte cover (Randall et al. 1996; McKenna and Castiglione 2010); and both physical habitat conditions and fish metrics such as fish biomass, diversity, and condition indices (Randall et al. 1996, 1998).

We calculated REI as the directional percent frequency multiplied by the fetch distance and the mean wind speed (Keddy 1982) for 36 wind direction classes in 10-degree increments starting at 0° for the years 2006–2014 at wind buoys on each lake (seven in Lake Huron, two each in Lakes Michigan and Ontario, one in Lake St. Clair, two in Lake Erie, and five in Lake Superior). The wind direction frequency and mean wind speed were summarized from buoy data obtained from NOAA National Buoy Data Center (http://www.ndbc.noaa.gov/) and Environment Canada and Climate Change. Using the methods and ArcGIS tool developed by Rohweder et al. (2012), REI was calculated for each lake applying the wind data summaries for the nearest buoy to a given area of lake, which were then combined into a Great Lakes-wide REI map for coastal margin and shallow nearshore zones. We classified REI into low, moderate, and high using natural breaks. We evaluated REI natural breaks with hydrodynamic waves models developed for Lake Erie and found generally good agreement between the two data sets (P. Zuzek, Zuzek Inc., personal communication, 2014).

For deep nearshore and deep to profundal offshore zones, we summarized published Great Lakes circulation patterns to map general patterns of surface water motion (Sheng and Rao 2006; Prakash et al. 2007; Schwab et al. 2009; Bennington et al. 2010; Beletsky et al. 2013). Currents in the Great Lakes influence the transport of particles including larval fish from nearshore to offshore and along the shore, a factor affecting fish recruitment and distributions within the lakes (Beletsky et al. 2007). The directional (alongshore) current was defined as occurring from the 5 m isobaths to either the 30 m isobaths (15 m in Lake Erie) or 5 km from the high-resolution shoreline, whichever distance was greater (Table 3; Fig. 2) based on a compilation of studies and information describing circulation patterns (Beletsky et al. 1999; Rao and Schwab 2007; Kelly et al. 2015; C. Troy, Purdue University, personal communication, 2015). The large-scale cyclonic–anticyclonic and mixed circulation patterns were mapped from the directional current boundary across the offshore zone using heads-up digitizing.

Tributary influence

The tributary influence variable represents the potential influence of tributary and coastal watersheds on coastal and nearshore zones. This variable was computed by first calculating the contributing watershed area of each tributary or coastal segment. Three classes of the tributary influence variable were used, based on tributary catchment area (Minns and Wichert 2005; Allan et al. 2013): low (<30 km², mean size of first- and second-order tributaries); moderate (30–250 km², representing third- and some fourth-order tributaries), and high (>250 km², representing ≥fourth-order tributaries; Table 2; Fig. 2). This variable was developed for the nearshore zones only, and offshore zones were assigned a value of "0".

The relative tributary size was then propagated into the lake based on a mathematical distance decay function weighted by depth. The decay equation assumed 10% of the initial flow value persisted at 15 km from the river mouth and 1% at 30 km distance (Allan et al. 2013), but was modified to weight distance by depth to allow the load to move more easily through shallow waters (<5 m) and become entrained in the nearshore zone (Makarewicz et al. 2012). For the tributaries, the distance was calculated from the pour-point of each river mouth; for the coastal segments without tributaries, the distance was from the midpoint of the entire interfluve shoreline. To capture the flow of the connecting channels, we assigned an estimated watershed area based on the proportion of major contributing watersheds for each connecting channel (St. Marys, North Channel, St. Clair, Detroit, and Niagara Rivers). For St. Marys, Detroit, and Niagara Rivers, we captured the influence of the contributing lake by further scaling it to the mean flow.

Spatial data aggregation and mapping

The spatial data used to develop the ecological classification were obtained from the GLAHF GIS raster-based spatial structure and relational geodatabase that has three nested grid cell sizes (9000, 1800, and 30 m) and unique identifiers for all grid cells (Wang et al. 2015). All data layers discussed in this study were processed with GLAHF spatial standards: (*i*) data were updated to the standard projection (USA Contiguous Albers Equal Area Conic projection, USGS version) and 30 m cell size using the Project Raster Tool; (*ii*) data gaps for depth and CDD due to differences in spatial resolution within the data extent were filled using the Euclidean Allocation Tool; (*iii*) data were masked by the GLAHF shoreline delineation; and (*iv*) binational harmonized tributary watersheds, pour-points, and shorelines from the Great Lakes Hydrography Dataset (GLHD; Forsyth et al. 2016) were integrated with the coastal and nearshore zones. All data layers were processed using ESRI (2015) ArcGIS for Desktop 10.3.1 and Python 2.7.

The AEUs were created by overlaying the maps of the four variables and assigning a four-digit code to each local cell (30 m) by concatenating class values of bathymetry, CDD, mechanical energy, and tributary influence (in that order; McKenna and Castiglione 2010). Each unique four-digit code represented a distinct AEU type and was assigned a unique color (D. Brenner, University of Michigan, personal communication, 2017; Sayre et al. 2014). Contiguous areas of the same AEU code were designated as patches of that AEU type. Postprocessing of AEU patches included merging small isolated polygons created as an artifact of rasterized data with larger contiguous polygons connected by vertices and edges. The resulting mosaic of ecotype patches may be used to describe and quantify the extent and distribution of various basic ecological conditions throughout the Great Lakes basin at different spatial scales (e.g., basin-wide, lake basin, or sub-basin and within local areas of a lake such as a river mouth or bay).

Results

The mapped AEU product is a hierarchical combination of standardized data layers that is the first consistent geographical classification and mapping of all five Laurentian Great Lakes (Fig. 3). Seventy-seven unique combinations of the descriptor variables (AEU types) were identified throughout the Great Lakes basin. After postprocessing, there were 1997 AEU polygons (patches of each AEU type) ranging from 1 to >48 000 km^2, with a mean size of 123 km^2 (standard deviation (SD) 1282.65 km^2) and median size of 5 km^2 (median absolute deviation 5.309 km^2). Approximately 1280 AEU patches were between 1 and 10 km^2 and were located in the coastal and nearshore zones (Table 3). Large AEU polygons (>1000 km^2) were located predominantly in the offshore zones.

Frequency and spatial extent of AEUs

These AEUs identify and characterize units of the lakes that have distinct combinations of physical factors that drive ecological processes and higher function with factor thresholds based on ecologically relevant information when available. Each AEU patch represents a group of 30 m (coastal and nearshore) or 1800 m horizontal cells (offshore) with the same set of bathymetry, CDD, mechanical energy, and tributary influence conditions. For example AEU code "1312" indicates coastal margin (bathymetry = 1), low CDD (CDD = 3), low relative exposure (mechanical energy = 1), and moderate tributary influence (tributary influence = 2). Several of the possible four-variable combinations did not occur, such as deep water over 100 m and high CDD, and thus are not found in the final AEU combinations.

Comparisons of AEUs among lakes

A broad picture of the Great Lakes classification shows that Lakes Superior and Erie are generally different from the other lakes (Figs. 3 and 4), Lakes Michigan and Ontario share many AEUs in common, and Lake Huron is a mix of the other four lakes. Distribution of the 77 AEU types varied by lake, by lake sub-basin, and by ecological zones (Table 4). Across the basin, the number of AEUs was highest in the nearshore (35), followed by the coastal margin (26), and lowest in the offshore (16). Lake Huron had the highest numbers of AEUs (61), followed by Lakes Michigan (48), Superior (44), Ontario (43), and Erie (27). Within Lake Huron, the northern and North Channel – Georgian Bay sub-basins had the greatest diversity of AEUs (42 and 33, respectively), with the greatest richness of AEUs occurring in the nearshore zone of these sub-basins (16 and 20, respectively). The connecting channels had the lowest numbers of AEUs (Niagara River — 5, St. Mary's River — 8, and the St. Clair – Detroit River System — 13). Of the major bays, Green Bay of Lake Michigan had the most AEUs (21), followed by Saginaw Bay, Lake Huron (19), and Whitefish Bay, Lake Superior (18). The shallow western basin of Lake Erie (mean depth 8.27 m) had 11 AEUs, while the Bay of Quinte, Lake Ontario (mean depth 8.5 m) had 8 AEUs.

Three AEU types cover nearly half of the area of the Great Lakes (Figs. 3 and 4; Table A2). AEU 6150, characterized by profundal offshore depths, low CDD, and cyclonic and anticyclonic currents, represents 22% of the total area of the lakes and was unique to eastern Lake Superior and northern Lake Huron (58.1% and 10.2%, respectively; Figs. 5*b* and 5*d*). AEU 5250 and 6250, characterized respectively by deep and profundal offshore depths, moderate CDD, cyclonic and anticyclonic currents, each represent about 12% of the total area of the Great Lakes and were found predominantly in Lakes Michigan, Huron, and Ontario. The AEU types unique to only one lake represented about 7% of the total area of the Great Lakes and were identified in Lakes Superior, Michigan, and Erie. The AEU types located only in Lake Erie represented 5.7% of the entire basin and were characterized by shallow offshore depths (unique to Lake Erie), moderate to high CDD, and mixed directional and cyclonic currents (e.g., AEUs 4250, 4260, 4350, and 4360). Unique units in Lake Superior were less than 2% of the total area of the Great Lakes, typically located in the coastal margin zone, and characterized by low CDD with high relative exposure and mixed tributary influences (e.g., AEUs 1122 to 2133) or by profundal depths and low CDD with directional currents (AEU 6140). Unique units in Lake Michigan were located primarily in the southern basin in coastal margin and shallow nearshore areas, with high CDD, high exposure, and moderate tributary influence (<1% of total Great Lakes area; AEUs 1332 and 2332, respectively).

Approximately 32% of the areal extent of AEUs were common to all lakes except Lake Superior, and 13% were common to all lakes except Lake Erie; no AEUs were common to all five lakes. For all lakes, one to three AEU types accounted for over 50% of the total area of that lake (Fig. 4; Table A2). The AEU type 6150 in Lake Superior (profundal offshore, low CDD, and cyclonic currents) accounted for 58% of the lake, and AEU types 6250 and 5250 (profundal and deep offshore, moderate CDD, and cyclonic currents) in Lakes Michigan and Ontario accounted for approximately 58% of each lake. In Lake Huron, types 6150, 5250, and 5160 accounted for about 41% of the lake area (a mix of profundal and deep offshore depths, low and moderate CDD, and cyclonic and mixed circulations patterns). The AEU type 4350 (shallow offshore, high CDD, moderate exposure, and no tributary influence) was unique to Lake Erie and accounted for about 26% area of the lake.

Assessment of relatively distinct AEUs

The ecosystem mapping of AEUs not only illustrates the spatial distribution and extent of different types of ecological units across the basin (Figs. 3 and 4), but also facilitates comparison of unique areas throughout the Great Lakes to identify similarities and differences due to key drivers of ecological condition (Figs. 5 and 6). For example, Saginaw Bay of Lake Huron, Green Bay of Lake Michigan, and the western sub-basin of Lake Erie are three large shallow bays with high tributary influence. Saginaw Bay and

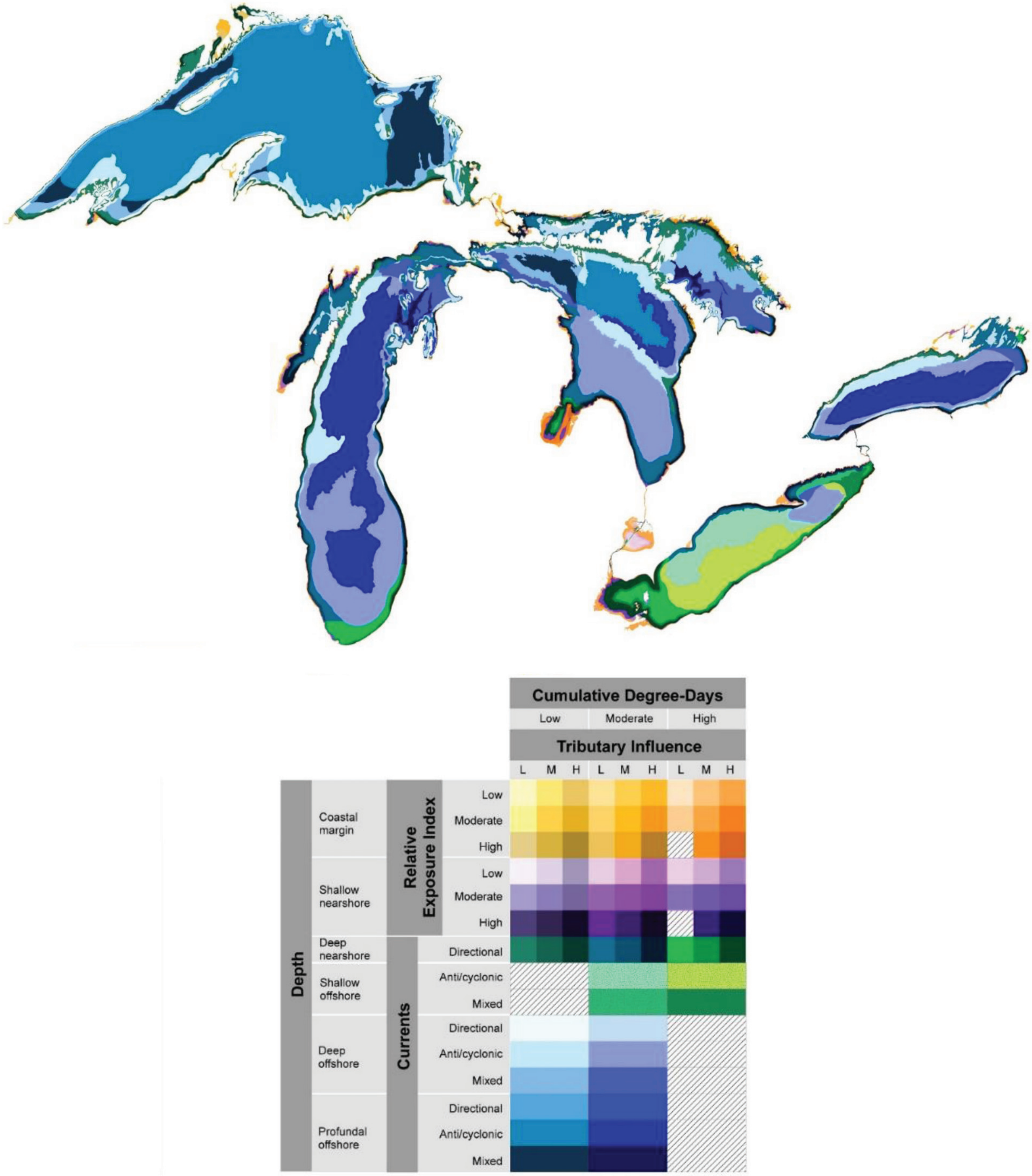
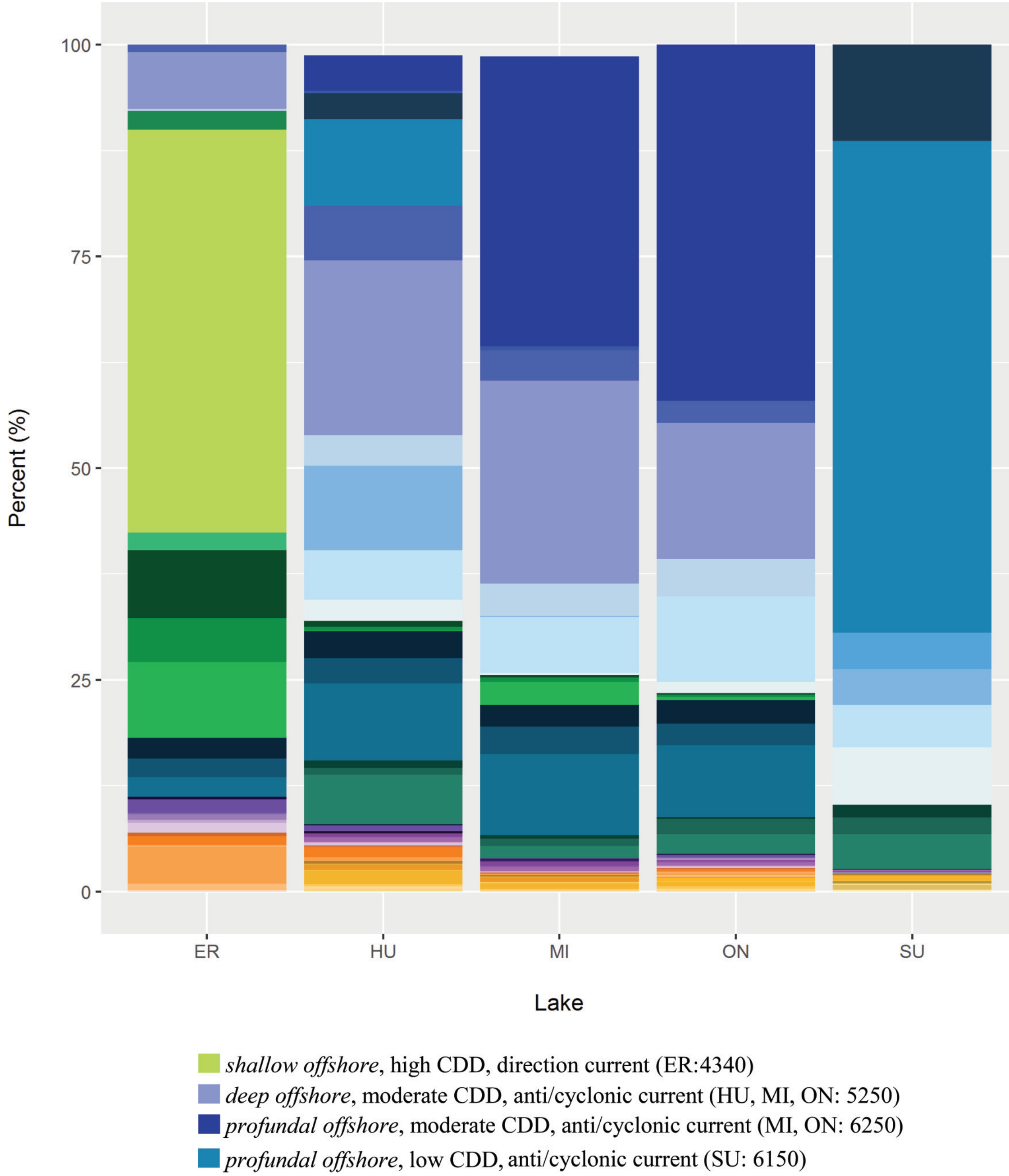


Fig. 3. Ecosystem-based mapping of aquatic ecological units of the Great Lakes. Four variables were combined hierarchically across three ecological zones (coastal margin, nearshore, and offshore) as shown in the legend: depth, cumulative degree-days, mechanical energy (i.e., relative exposure index and currents), and tributary influence. Each variable was characterized by three or four criteria that defined ecological breaks in key drivers. Each aquatic ecological unit (AEU) type is shown by a unique color.

the western sub-basin of Lake Erie had five out of 35 total AEUs in common, which represented 49.3% of the area of Saginaw Bay and 86.5% of the western sub-basin of Lake Erie (Figs. 5*f*, 5*g*, 5*h*, and 6*a*). Similarly, seven out of 35 AEUs were common to Green Bay and Saginaw Bay, representing 86.9% and 29.2% of the total areas of these bays, respectively. In addition, the outer portion of Saginaw Bay and Green Bay include deeper, moderate CDD types that covered about 10% of each bay. Only two AEU types were common to all three areas representing 1.3%, 7.6%, and 12.4% of Green Bay, Saginaw Bay, and the western sub-basin of Lake Erie.

The distribution and extent of these AEUs reflect both the similarities and differences among these three areas of the Great Lakes (Figs. 5*f*, 5*g*, 5*h*, and 6*a*). All three bays similarly receive input from large tributaries (Saginaw, Maumee, and Fox Rivers), which was reflected in AEU types; approximately 60% of the AEU patches in both the Saginaw Bay and western sub-basin of Lake Erie and

Fig. 4. Bar graph illustrating the relative area of different aquatic ecological units (AEUs) across the five Great Lakes. Lake codes are in Fig. 1. The color codes match the codes for AEU types in Fig. 3. For reference, the dominant AEU types are listed in the figure legend.



37% of AEU patches in Green Bay were characterized by high tributary influence. These three bays differed in the amount of coastal margin patches, with Saginaw Bay having a higher percentage than either the western basin of Lake Erie or Green Bay (28.8% versus 13.7% and 11.3%, respectively), and also the amount of deep nearshore patches, with the western sub-basin of Lake Erie and Green Bay having a higher proportion than Saginaw Bay (77%, 69%, and 49%, respectively). In general, Green Bay and Saginaw Bay had a greater diversity of AEU types than did western Lake Erie (21, 19, and 11 AEUs, respectively). Western Lake Erie and Green Bay were dominated by three to four types of deep nearshore AEUs (69% and 77% of total area, respectively), while Saginaw Bay AEUs were more evenly distributed (e.g., six types of deep nearshore AEUs that covered about 50% of the total bay area).

To further compare similarities and differences between unique areas in the Great Lakes we compared the northern sub-basins of Lakes Michigan and Huron and eastern sub-basin of Lake Superior. The northern sub-basin of Lake Huron and eastern sub-basin of Lake Superior had 14 AEUs in common, representing 85.3% and 67.8% of total sub-basin area, respectively (Figs. 5*b*, 5*d*, and 6*b*; Table A2). The northern sub-basins of Lakes Huron (NHU and EHU) and Michigan (NMI and NCMI) had 16 AEU types in common that included two deep nearshore and three deep offshore AEU types that covered substantive portions of these northern sub-basins (29.05% and 80.74% of northern Lakes Huron and Michigan, respectively) and coastal margin and shallow nearshore units that represent a small portion of each lake (11 AEUs; Figs. 5*c*, 5*d*, and 6*b*). The north-central sub-basin of Lake Michigan was

Table 4. Distribution of AEU types by lake, sub-basin, and aquatic zones shown in Fig. 1.

	Total	CM	NS	OS
Great Lakes Basin	77	26	35	16
Erie	27	7	13	7
CER	20	5	11	4
EER	19	3	9	7
LSC	11	3	8	0
WER	11	4	7	0
Huron	61	20	30	11
CHU	26	8	12	6
EHU	24	8	10	6
NCGeB	33	11	16	6
NHU	42	13	20	9
SB	19	5	13	1
SMR	8	1	6	1
Michigan	48	15	24	9
CMI	18	4	10	4
GrB	21	7	12	2
NCMI	33	9	15	9
NMI	29	9	15	5
SMI	22	7	13	2
Ontario	43	14	23	6
CON	31	11	14	6
EON	34	12	18	4
NR	5	2	3	0
WON	20	5	10	5
Superior	44	18	20	6
CSU	37	14	17	6
ESU	36	15	15	6
WB	18	8	8	2
WSU	19	6	7	6

Note: Aquatic zones: CM, coastal margin; NS, nearshore; OS, offshore. For location acronyms, refer to Fig. 1.

dominated by AEU type 6250 (55.3%; profundal offshore depths, moderate CDD, and cyclonic currents), which also covered a substantive portion of the eastern sub-basin of Lake Huron (26.6%). However, only seven AEU types were common to all of these northern sub-basins, and they accounted for relatively small percentages of the sub-basin areas. These results support the notion that Lakes Michigan and Huron are similar in ecotype and supply but also identify unique aspects to each lake and highlight the commonality between northern Lake Huron and eastern Lake Superior. The eastern basin of Lake Ontario shares 10 AEUs with the northern basin of Lakes Michigan and Huron, representing about 65% of its area (Figs. 5*c*, 5*d*, 5*e*, and 6*b*) predominated by AEU 3241 (39% of eastern Lake Ontario; deep nearshore, moderate CDD, directional currents, and low tributary influence) that is most in common with the northern Michigan sub-basin (34%).

The results of this classification and mapping include GIS layers of the mapped AEUs and individual layers that were used for classification and are publicly available at www.glahf.org/classification/.

Discussion

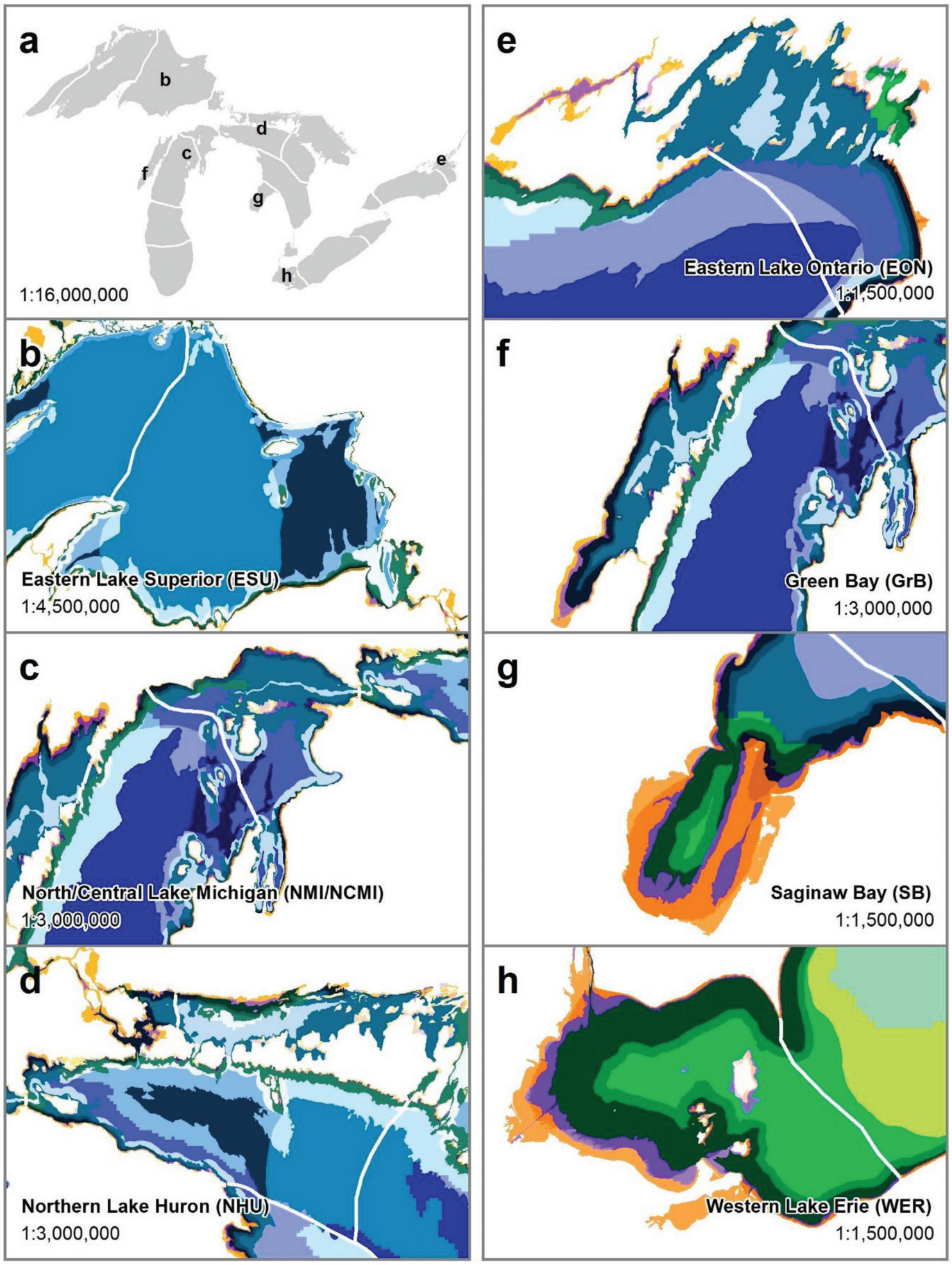
Comparison and justification

We describe the methodology and results of an ecological classification and mapping of Great Lakes ecosystems. Our goal was to develop an ecological classification that would be useful for a variety of purposes, could be applied at a variety of spatial scales, and could be mapped across the entire Great Lakes Basin with existing data and knowledge. Ecological classification often uses both abiotic and biotic characteristics to delineate ecosystems or ecological units (Barnes et al. 1982; Rowe 1991). For example, terrestrial ecosystems have been delineated using climate, geology, and forest community types (Barnes et al. 1982; Albert et al. 2005). We did not use biological data directly to identify units, in part because those data are scarce given the large expanse of the Great Lakes and the limited areas that are sampled. In addition, unlike terrestrial ecosystems, biological data in aquatic systems often exhibit high temporal and spatial variability, making them challenging to use for delineating ecosystem boundaries. Instead, we used a top-down approach to identify ecological units informed by evaluating physical–biological relationships where data were available. We used these relationships to identify key drivers and relevant thresholds, resulting in a natural classification system (Bailey 2009).

Other methods for ecosystem classification and unit mapping range from boundaries drawn according to implicit judgment based on visual appearances to a suite of more explicit, systematic approaches using map overlays or multivariate clustering to integrate ecosystem data into units (Bailey 2009). Classifications defined by implicit judgment use a gestalt method to map units based on visual assessment and expert knowledge at limited geographic locations, which does not necessarily incorporate the controlling forces that differentiate ecosystem types in a systematic defensible way or at larger scales. An example of this method would be drawing a polygon around a known location to identify boundaries for an ecosystem type. Because there are no objective ecological rules for setting unit boundaries using the gestalt method, the resulting unit types vary geographically, are difficult to implement regionally or compare across a region, and have limited ecological relevance and predictive ability. The map overlay approach links available maps of classed factors to define unit boundaries. This method can be useful for ecosystem mapping but may present shortcomings if maps for key ecosystems factors are not available, if the rules for determining classes are not objective, or if classed factor boundaries do not relate to ecosystem processes. Ecological units have been defined by various statistical multivariate clustering methods applied to biotic and abiotic variables, typically spatial data in GIS format, to empirically identify clusters of cells that are similar relative to biological response variables (Omi et al. 1979; Rowe 1991). This method requires obtainable biological response variables and may result in unit boundaries that do not reflect hierarchical ecosystem drivers (Rowe and Sheard 1981; Bailey 2014).

Our approach was to identify multiple causal factors and ecologically relevant criteria to create a natural classification system (or genetic, sensu Bailey 2009) that reflects our understanding of the structure and function of Great Lakes ecosystems. This resulted in a general, multipurpose classification system that identified functionally similar units defined by large-scale drivers in an ecosystem context, not by geographic locations, and thus is independent of place. This approach drew upon the principles of ecosystem geography that recognizes the hierarchical structure of ecosystems (Allen and Starr 1982). Ecosystem geography emphasizes the use of multiple, coarse-scale variables that are causally linked or that constrain finer-scale patterns and processes to develop generalized classifications and identify and map ecosystem boundaries (Bailey 2009, 2014). This approach has a long history in terrestrial (Bailey 2009; Barnes et al. 1982; Cleland et al. 1997; Klijn and Haes 1994), riverine (Frissell et al. 1986; Hawkins et al. 1993; Seelbach and Wiley 2005; Seelbach et al. 2006; Brenden et al. 2008), inland lake (Gassner et al. 2005; Soranno et al. 2010; Wehrly et al 2012), and more recently marine (Guarinello et al. 2010) ecological classification and mapping but has had limited application in the Laurentian Great Lakes (but see McKenna and Castiglione 2017). This approach for terrestrial ecosystems typically results in land unit classifications that are more generic than other methods, but have greater utility for multiple purposes, including assessment of ecosystem services or climate change impacts and resource management (Groves 2003; Albert et al. 2005; Sowa et al. 2007; Sayre et al. 2014).

Fig. 5. Inset maps from five focal areas that represent a range of aquatic ecological units (AEUs) with similar conditions occurring in different lakes and lake sub-basins (see Fig. 1 for sub-basin abbreviations; see Fig. 3 for color codes).

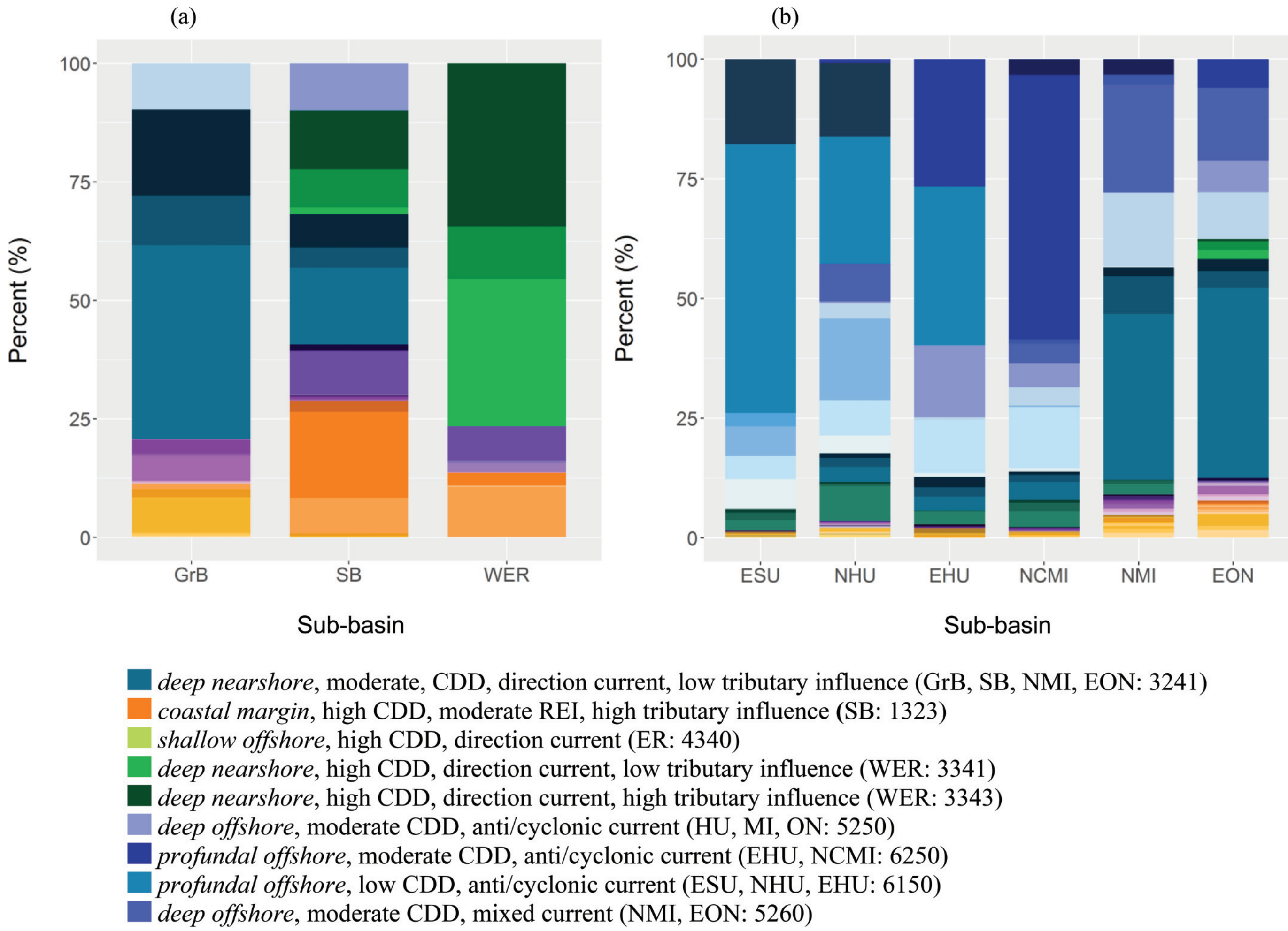


Potential utility–application

Because our classification was developed without anthropogenic variables, the resulting spatial units can provide a framework for establishing baselines of ecosystem potential (sensu Warren 1979), which can be used to assess deviation from expected conditions and set ecological restoration targets (Frissell et al. 1986; Riseng et al. 2006). The classification can also serve as a framework for developing physical, chemical, and biological criteria, as has been done for terrestrial ecosystems (Omernik 1987; Kurtz et al. 2006). The AEUs could also be used to develop stratified sampling designs for monitoring programs seeking to assess the condition of Great Lakes nearshore and offshore waters, which is a requirement of the most recent Great Lakes Water Quality Agreement (GLWQA 2012).

Classifications like ours can also be used for setting environmental policy. For instance, ecological classification systems (Cowardin et al. 1979; Brinson 1993) are specifically incorporated into policies that regulate conversion and compatible uses of wetlands under section 404 of the US Clean Water Act (P.L. 95-217). Ecological classifications have also been used for developing management goals and guidelines. For instance, the United States Department of Agriculture soil classification system has been used for decades as a framework for assessing suitability of land for cultivation and developing recommendations and guidelines for management practices to maintain soil health and reduce runoff and loss of sediments and nutrients (USDA 1961). Similarly, the USDA Forest Service's ecological unit classification system has served as the foundation for developing forest management goals, objectives, and strategies (Winthers et al. 2005). Our nearshore AEUs could be used in a similar manner to these classifications for establishing shoreline development capability classes to inform assessment and planning performed under policies and programs

Fig. 6. Bar graphs illustrating the proportion of different aquatic ecological units (AEUs) across five focal areas mapped in Fig. 5; the color codes match the codes for the AEUs in Fig. 3. (*a*) Comparison of Green Bay (GrB, Lake Michigan), Saginaw Bay (SB, Lake Huron), and western sub-basin of Lake Erie (WER). (*b*) Comparison of the eastern sub-basin of Lake Superior (ESU), northern and eastern sub-basins of Lake Huron (NHU, EHU), north-central and north sub-basins of Lake Michigan (NCMI, NMI), and eastern Lake Ontario with Bay of Quinte (EON). Lake codes are in Fig. 1. The color codes match the codes for AEU types in Fig. 3. For reference, the dominant AEU types in this figure are listed in the figure legend.



like the NOAA's Coastal Zone Management Act of 1972 (P.L. 92-583). The AEUs could also be used to help develop general management guidelines for the proper placement and selection of coastal green infrastructure practices and could be incorporated into tools like the Great Lakes Coastal Resilience Guide (http://greatlakesresilience.org/).

This Great Lakes classification also has utility for research and modeling to advance our understanding and improve our ability to forecast ecosystem responses across the Great Lakes. Goldstein and Goldstein (1978) pointed out 40 years ago that good classifications make discoveries possible, and in turn, these discoveries change our way of classifying the things we study. It is our hope that our AEUs will be correctly viewed as testable hypotheses and used to develop experimental designs and incorporated as potential high-level explanatory variables in statistical analyses. Doing so will help advance our understanding of physical, chemical, and biological patterns and processes within and among these larger ecosystem units and possibly identify new thresholds to improve the classification in the future. For example, embayments such as the western basin of Lake Erie, Saginaw Bay (Lake Huron), and Green Bay (Lake Michigan) are often thought of as ecologically similar areas because they are shallow, sheltered from the wind, and have high tributary influence. Similarly, the northern basins of Lakes Huron and Michigan are often considered to be one unit similar to the eastern basin of Lake Superior. Our classification shows that there are similarities, but also differences in the amount and types of AEUs, suggesting that they may have different ecological potential and may respond differently to perturbations and management actions. This hypothesis could be tested by developing sampling designs that stratify physicochemical and biological data collection across different AEUs to characterize ecosystem services or resources or by applying and comparing similar management actions across different AEUs. Because our classification is based on ecosystem drivers, it provides important ecological context that can help predict ecological patterns at finer spatial scales (Sowa et al. 2007). More specifically, our classification could be incorporated into existing or new lake ecosystem models developed for the Great Lakes (Chapra et al. 2016; Bocaniov et al. 2016; Verhamme et al. 2016) and help improve our ability to forecast ecosystem responses across the Great Lakes.

Finally, this classification reflects the fact that ecosystem patterns are hierarchically organized. Jensen et al. (2001) developed a generalized scale for classifying and assessing biophysical environments that related hierarchical land-based classification scales to existing classifications for riverine and lacustrine systems. Our classification describes patterns at a coarse scale and generates a lake mosaic (sensu landscape mosaic; Bailey 2009) of contiguous mapped patches (polygons) whose descriptive characteristics are not place-dependent and would be akin to a land type association, land type, and riverine valley bottom, lake type, or lake zone.

Potential limitations

Our Great Lakes classification was developed at a practical scale for management to address broadscale variability across the lakes and also fine-scale complexity in the nearshore and coastal areas. As we just discussed, we believe our classification has broad utility for research and management. However, it may not be applicable for specific purposes such as characterizing habitat suitability for a particular species or site-specific analyses or local conditions, which could be variable at a finer spatial and temporal scales (Rowe 1991; Huggett 1995). Rather, our classification may be best suited for providing a standard geographic unit for assessing ecosystem services, studying spatial variability in the effects of climate change, or for resource conservation and management across the basin (Sowa et al. 2007; Sayre et al. 2014). Other variables such as basin-wide substrate could enhance the ecosystem classification. Substrate is a biologically relevant variable, which can act independently from other variables due to the glaciation history of the upper Midwest and tributary influences but in some areas is changing due to anthropogenic influences especially in the nearshore. Practically, substrate data was not consistently available for all areas of the Great lakes so could not be incorporated into a classification at this time.

Summary

Ecosystem classification and mapping is an approximation and generalization of ecosystem structure and function based on our best understanding and measurement of natural phenomena. We have developed a classification that simplifies the Great Lakes into a limited set of ecosystem types to aid in research and management of this expansive freshwater system. Our ecosystem classification is based on the concept that dominant physical processes acting at broad scales describe distinct, homogeneous ecological units. Again, this classification system represents a hypothesis that needs to be evaluated independently with physical, chemical, and biological data to test the underlying premise that units defined by large-scale physical factors are functionally different and that areas of the same class will respond similarly to comparable management actions (Bailey 1983). Our classification and mapping of AEUs for the Great Lakes and its associated spatial data are publicly available and can be downloaded as GIS layers (http://glahf.org/classification/). This aquatic classification and mapping of the entire Great Lakes is a first-generation product developed using best available data. As new spatial data and models are developed with finer spatial scales, we expect this classification will be updated and improved. The classification allows us, for the first time, to characterize ecosystem types, their spatial extent, and distribution across the Great Lakes and can be used to characterize similarity and differences within and among the Great Lakes — a novel and powerful tool for communication, research, and ecosystem-based management.

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References

Albert, D.A., Wilcox, D.A., Ingram, J.W., and Thompson, T.A. 2005. Hydrogeomorphic classification for Great Lakes coastal wetlands. J. Gt. Lakes Res. **31**(S1): 129–146. doi:10.1016/S0380-1330(05)70294-X.

Allan, J.D., McIntyre, P.B., Smith, S.D.P., Halpern, B.S., Boyer, G.L., Buchsbaum, A., Burton, G.A., Campbell, L.M., Chadderton, W.L., Ciborowski, J.J.H., Doran, P.J., Eder, T., Infante, D.M., Johnson, L.B., Joseph, C.A., Marino, A.L., Prusevich, A., Read, J.G., Rose, J.B., Rutherford, E.S., Sowa, S.P., and Steinman, A.D. 2013. Joint analysis of stressors and ecosystem services to enhance restoration effectiveness. Proc. Natl. Acad. Sci. U.S.A. **110**(1): 372–377. doi:10.1073/pnas.1213841110.

Allen, T.F., and Starr, T.B. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago.

Auer, M.T., Auer, N.A., Urban, N.R., and Auer, T. 2013. Distribution of the amphipod *Diporeia* in Lake Superior: the ring of fire. J. Gt. Lakes Res. **39**: 33–46. doi:10.1016/j.jglr.2012.12.020.

Bailey, R.G. 1983. Delineation of ecosystem regions. Environ. Manage. **7**(4): 365–373. doi:10.1007/BF01866919.

Bailey, R.G. 2009. Ecoregions: the ecosystem geography of the oceans and continents. 2nd ed. Springer LLC, New York. doi:10.1007/978-1-4939-0524-9.

Bailey, R.G. 2014. Ecosystem geography: from ecosystem to sites. 2nd ed. Springer LLC, New York. doi:10.1007/978-0-387-89516-1.

Bailey, R.M., Latta, W.C., and Smith, G.R. 2004. An atlas of Michigan fishes with keys and illustrations for their identification. University of Michigan Museum of Zoology.

Barnes, B.V., Pregitzer, K.S., Spies, T.A., and Spooner, V.H. 1982. Ecological forest site classification. J. For. **80**: 493–498.

Beletsky, D., Saylor, J.H., and Schwab, D.J. 1999. Mean circulation in the Great Lakes. J. Gt. Lakes Res. **25**(1): 78–93. doi:10.1016/S0380-1330(99)70718-5.

Beletsky, D., Mason, D.M., Schwab, D.J., Rutherford, E.S., Janssen, J., Clapp, D.F., and Dettmers, J.M. 2007. Biophysical model of larval yellow perch advection and settlement in Lake Michigan. J. Gt. Lakes Res. **33**: 842–866. doi:10.3394/0380-1330(2007)33[842:BMOLYP]2.0.CO;2.

Beletsky, D., Hawley, N., and Rao, Y.R. 2013. Modeling summer circulation and thermal structure of Lake Erie. J. Geophys. Res. Oceans, **118**: 6238–6252.

Bennett, E.B. 1978. Characteristics of the thermal regime of Lake Superior. J. Gt. Lakes Res. **4**(3–4): 310–319. doi:10.1016/S0380-1330(78)72200-8.

Bennington, V., McKinley, G.A., Kimura, N., and Wu, C.H. 2010. General circulation of Lake Superior: mean, variability, and trends from 1979 to 2006. J. Geophys. Res. **115**: C12015. doi:10.1029/2010JC006261.

Bocaniov, S.A., Leon, L.F., Rao, Y.R., Schwab, D.J., and Scavia, D. 2016. Simulating the effect of nutrient reduction on hypoxia in a large lake (Lake Erie, USA–Canada) with a three-dimensional lake model. J. Gt. Lakes Res. **42**(6): 1228–1240. doi:10.1016/j.jglr.2016.06.001.

Brazner, J.C., Danz, N.P., Trebitz, A.S., Niemi, G.J., Regal, R.R., Hollenhorst, T., Host, G.E., Reavie, E.D., Brown, T.N., Hanowski, J.M., Johnston, C.A., Johnson, L.B., Howe, R.W., and Ciborowski, J.J.H. 2007. Responsiveness of Great Lakes wetland indicators to human disturbances at multiple spatial scales: a multi-assemblage assessment. J. Gt. Lakes Res. **33**: 42–66. doi:10.3394/0380-1330(2007)33[42:ROGLWI]2.0.CO;2.

Brenden, T.O., Wang, L., and Seelbach, P.W. 2008. A river valley segment classification of Michigan streams based on fish and physical attributes. Trans. Am. Fish. Soc. **137**: 1621–1636. doi:10.1577/T07-166.1.

Brinson, M.M. 1993. A Hydrogeomorphic classification for wetlands. US Army Corps of Engineers, Washington, D.C. Wetlands Research Program Technical Report WRP-DE-4.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., and West, G.B. 2004. Toward a metabolic theory of ecology. Ecology, **85**: 1771–1789. doi:10.1890/03-9000.

Busch, W.-D.N., and Lary, S.J. 1996. Assessment of habitat impairments impacting the aquatic resources of Lake Ontario. Can J. Fish. Aquat. Sci. **53**(S1): 113–120. doi:10.1139/f96-005.

Busch, W.-D.N., and Sly, P.G. (*Editors*). 1992. The development of an aquatic habitat classification system for lakes. CRC Press, Boca Raton, Fla.

Chapra, S.C., Dolan, D.M., and Dove, A. 2016. Mass-balance modeling framework for simulating and managing long-term water quality for the lower Great Lakes. J. Gt. Lakes Res. **42**(6): 1166–1173. doi:10.1016/j.jglr.2016.04.008.

Chu, C., Koops, M.A., Randall, R.G., Kraus, D., and Doka, S.E. 2014. Linking the land and the lake: a fish habitat classification for the nearshore zone of Lake Ontario. Freshw. Sci. **33**(4): 1159–1173. doi:10.1086/678228.

Cleland, D.T., Avers, P.E., McNab, W.H., Jensen, M.E., Bailey, R.G., King, T., and Russell, W.E. 1997. National hierarchical framework of ecological units. *In* Ecosystem management applications for sustainable forest and wildlife resources. *Edited by* M.S. Boyce and A. Haney.Yale University Press, New Haven, Conn. pp. 181–200.

Cooper, M.J., Lamberti, G.A., and Uzarski, D.G. 2014. Spatial and temporal trends in the invertebrate communities of Great Lakes coastal wetlands, with emphasis on Saginaw Bay of Lake Huron. J. Gt. Lakes Res. **40**(1): 168–182. doi:10.1016/j.jglr.2013.12.003.

Cowardin, L.M., Carter, V., Golet, F.C., and LaRoe, E.T. 1979. Classification of wetlands and deepwater habitat of the United States. Fish and Wildlife Service, US Department of the Interior, Washington, D.C.

Csanady, G.T. 1970. Dispersal of effluents in the Great Lakes. Water Res. **4**: 79–114. doi:10.1016/0043-1354(70)90022-9.

Danz, N.P., Niemi, G.J., Regal, R.R., Hollenhorst, T., Johnson, L.B., Hanowski, J.M., Johnston, C., Axler, R., Ciborowski, J., Hrabik, T., Brady, V.J., Kelly, J.R., Brazner, J.C., and Howe, R.W. 2007. Integrated measures of anthropogenic stress in the U.S. Great Lakes Basin. Environ. Manage. **39**: 631–647. PMID: 17387547.

Eadie, B.J., Schwab, D.J., Johengen, T.H., Lavrentyev, P.J., Miller, G.S., Holland, R.E., Leshkevich, G.A., Lansing, M.B., Morehead, N.R., Robbins, J.A., Hawley, N., Edgington, D.N., and Van Hoof, P.L. 2002. Particle transport, nutrient cycling, and algal community structure associated with a major winter–spring sediment resuspension event in southern Lake Michigan. J. Gt. Lakes Res. **28**: 324–337. doi:10.1016/S0380-1330(02)70588-1.

Elrashidi, M.A., West, L.T., Seybold, C.A., and Peaslee, S.D. 2014. Application of soil survey to assess nonpoint source of contamination to surface water in agricultural watersheds: heavy metals and alkaline earth elements. United States Department of Agriculture, Natural Resources Conservation Service, National Soil Survey Center, Soil Survey Investigations Report No. 54.

Federal Geographic Data Committee. 2012. Coastal and marine ecological classification standard (CMECS), Version 6(Final) [online]. FGDC-STD-018-2012. https://www.fgdc.gov/standards/projects/cmecs-folder/CMECS_Version_06-2012_FINAL.pdf [accessed 9 May 2017].

Fetzer, W.W., Roth, B.M., Infante, D.M., Clapp, D.F., Claramunt, R.M., Fielder, D.G., Forsyth, D.K., He, J.X., Newcomb, T.J., Riseng, C.M., Wehrly, K.E., and Zorn, T.G. 2017. Spatial and temporal dynamics of nearshore fish communities in Lake Michigan and Lake Huron. J Gt. Lakes Res. **43**: 319–334. doi:10.1016/j.jglr.2016.12.003.

Forsyth, D.K., Riseng, C.M., Wehrly, K.E., Mason, L.A., Gaiot, J., Hollenhorst, T., Johnston, C.M., Wyrzykowski, C., Annis, G., Castiglione, C., Todd, K., Robertson, M., Infante, D.M., Wang, L., McKenna, J.E., Jr., and Whelan, G. 2016. The Great Lakes Hydrography Dataset: consistent, binational watersheds for the Laurentian Great Lakes Basin. J. Am. Water Res. Assoc. **52**: 1068–1088. doi:10.1111/1752-1688.12435.

Frissell, C.A., Liss, W.J., Warren, C.E., and Hurley, M.S. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environ. Manage. **10**(2): 199–214. doi:10.1007/BF01867358.

Gassner, H., Wanzenbock, J., Zick, D., Tischler, G., and Pamminger-Lahnsteiner, B. 2005. Development of a fish based lake typology for natural Austrian lakes >50 ha based on the reconstructed historical fish communities. Int. Rev. Hydrobiol. **90**: 422–432. doi:10.1002/iroh.200510798.

Glyshaw, P.W., Riseng, C.M., Nalepa, T.F., and Pothoven, S.A.S. 2015. Temporal trends in condition and reproduction of quagga mussels (*Dreissena rostriformis bugensis*) in southern Lake Michigan. J. Gt. Lakes Res. **41**: 16–26. doi:10.1016/j.jglr.2015.08.006.

Goldstein, M., and Goldstein, I.F. 1978. How we know: An exploration of the scientific process. Plenum Press, New York.

GLWQA. 2012. Great Lakes Water Quality Agreement, Protocol Amending the Agreement between Canada and the United States of America on Great Lakes Water Quality, 1978, as Amended on October 16, 1983, and on November 18, 1987. Signed September 7, 2012 and entered into force February 12, 2013.

Groves, C. 2003. Drafting a conservation blueprint: a practitioner's guide to planning for biodiversity. Island Press, Washington, D.C.

Guarinello, M.L., Shumchenia, E.J., and King, J.W. 2010. Marine habitat classification for ecosystem-based management: a proposed hierarchical framework. Environ. Manage. **45**(4): 793–806. doi:10.1007/s00267-010-9430-5. PMID: 20119722.

Hansen, G.J.A., Read, J.S., Hansen, J.F., and Winslow, L.A. 2017. Projected shifts in fish species dominance in Wisconsin lakes under climate change. Global Change Biol. **23**(4): 1463–1476. doi:10.1111/gcb.13462.

Hawkins, C.P., Kershner, J.L., Bisson, P.A., Bryant, M.D., Decker, L.M., Gregory, S.V., McCulloch, D.A., Overton, C.K., Reeves, G.H., Steedman, R.J., and Young, M.K. 1993. A hierarchical approach to classifying stream habitat features. Fisheries, **18**(6): 3–12. doi:10.1577/1548-8446(1993)018<0003:AHATCS>2.0.CO;2.

Herdendorf, C.E., Hakanson, L., Jude, D.J., and Sly, P.G. 1992. A review of the physical and chemical components of the Great Lakes: a basis for classification and inventory of aquatic habitats. The development of an aquatic habitat classification system for lakes. CRC Press, Boca Raton, Fla. pp. 109–160.

Higgins, J.V., Bryer, M.T., Khoury, M.L., and Fitzhugh, T.W. 2005. A freshwater classification approach for biodiversity conservation planning. Conserv. Biol. **19**: 432–445. doi:10.1111/j.1523-1739.2005.00504.x.

Huggett, R.J. 1995. Geoecology: an evolutionary approach. Routledge, London.

Jensen, M.E., Goodman, I.A., Frissell, C.A., Brewer, C.K., and Bourgeron, P.S. 2001. Ecological classification and mapping of aquatic systems. *In* A guidebook for integrated ecological assessments. *Edited by* M.E. Jensen and P.S. Bourgeron. Springer Inc., New York.

Johnson, L., Ciborowski, J., Mackey, S., Hollenhorst, T., Gauthier, R., and Button, D.T. 2007. An integrated habitat classification and map of the Lake Erie basin. Final Report to National Fish and Wildlife Foundation.

Kalff, J. 2002. Limnology: inland water ecosystems. Prentice-Hall, Upper Saddle River, New Jersey.

Keddy, P.A. 1982. Quantifying within-lake gradients of wave energy: interrelationships of wave energy, substrate particle size and shoreline plants in Axe Lake, Ontario. Aquat. Bot. **14**: 41–58. doi:10.1016/0304-3770(82)90085-7.

Kelly, J.R., Yurista, P., Starry, M., Scharold, J., Bartsch, W., and Cotter, A. 2015. Exploration of spatial variability in nearshore water quality using the first Great Lakes national coastal condition assessment survey. J. Gt. Lakes Res. **41**: 1060–1074. doi:10.1016/j.jglr.2015.09.007.

Keough, J.R., Thompson, T.A., Guntenspergen, G.R., and Wilcox, D.A. 1999. Hydrogeomorphic factors and ecosystem responses in coastal wetlands of the Great Lakes. Wetlands, **19**: 821–834. doi:10.1007/BF03161786.

Klijn, F., and Haes, H.A. 1994. A hierarchical approach to ecosystems and its implications for ecological land classification. Landsc. Ecol. **9**: 89–104. doi:10.1007/BF00124376.

Kurtz, J.C., Detenbeck, N.D., Engle, V.D., Ho, K., Smith, L.M., Jordan, S.J., and Campbell, D. 2006. Classifying coastal waters: current necessity and historical perspective. Estuar. Coasts, **29**: 107–123. doi:10.1007/BF02784703.

Lane, J.A., Portt, C.B., and Minns, C.K. 1996. Spawning habitat characteristics of Great Lakes fishes. Can. MS Rep. Fish. Aquat. Sci. No. 2368.

Mackey, S.D. 2009. Nearshore habitats of the Great Lakes. *In* State of the Lakes Ecosystem Conference 2008 Background Paper. *Edited by* E.K. Hinchey and R. Cestaric. Nearshore Areas of the Great Lakes 2009. EPA 905-R-09-013 or Cat. No. En164-19/2009E-PDF. pp. 104–107.

Mackey, S.D. 2012. Great Lakes nearshore and coastal systems. *In* U.S. National Climate Assessment Midwest Technical Report [online]. *Coordinated by* J. Winkler, J. Andresen, J. Hatfield, D. Bidwell, and D. Brown. Available from http://greatlakesresilience.org/sites/default/files/library_reference_2012_GLISA_CoastalSectorMidWestTechnicalInputReportNationalClimateAssessment.pdf.

Magnuson, J.J., Webster, K.E., Assel, R.A., Bowser, C.J., Dillon, P.J., Eaton, J.G., Evans, H.E., Fee, E.J., Hall, R.I., Mortsch, L.R., Schindler, D.W., and Quinn, F.H. 1997. Potential effects of climate change on aquatic systems: Laurentian Great Lakes and Precambrian shield region. Hydrol. Process. **11**: 825–871. doi:10.1002/(SICI)1099-1085(19970630)11:8<825::AID-HYP509>3.0.CO;2-G.

Makarewicz, J.C., Lewis, T.W., Boyer, G.L., and Edwards, W.J. 2012. The influence of streams on nearshore water chemistry in Lake Ontario. J. Gt. Lakes Res. **38**: 62–71. doi:10.1016/j.jglr.2012.02.010.

Mason, L.A., Riseng, C.M., Gronewold, A.D., Rutherford, E.S., Wang, J., Clites, A., Smith, S.D.P., and McIntyre, P.B. 2016. Fine-scale spatial variation in ice cover and surface temperature trends across the surface of the Laurentian Great Lakes. Clim. Change, **138**: 71–83. doi:10.1007/s10584-016-1721-2.

McKenna, J.E., Jr., and Castiglione, C. 2010. Hierarchical multi-scale classification of nearshore aquatic habitats of the Great Lakes: Western Lake Erie. J. Gt. Lakes Res. **36**: 757–771. doi:10.1016/j.jglr.2010.09.005.

McKenna, J.E., Jr., and Castiglione, C. 2017. Hydrospatial Framework for the Laurentian Great Lakes. US Geological Survey. doi:10.5066/F76W99B2.

Meadows, G.A., Mackey, S.D., Goforth, R.G., Mickelson, D.M., Edil, T.M., Fuller, J., Guy, D.E., Jr., Meadows, L.A., Brown, E., Carman, S.M., and Liebenthal, D.L. 2005. Cumulative Habitat Impacts of Nearshore Engineering. J. Great Lakes Res. **31**(Supplement 1): 90–112.

Mehner, T., Holmgren, K., Lauridsen, L.T., Jeppesen, E., and Diekmann, M. 2007. Lake depth and geographical position modify lake fish assemblages of the European "central plains" ecoregion. Freshw. Biol. **52**: 2285–2297. doi:10.1111/j.1365-2427.2007.01836.x.

Minns, C.K., and Wichert, G.A. 2005. A framework for defining fish habitat domains in Lake Ontario and its drainage. J. Gt. Lakes Res. **31**: 6–27. doi:10.1016/S0380-1330(05)70287-2.

Neuheimer, A., and Taggart, C.T. 2006. The growing degree-day and fish size at age: the overlooked metric. Can. J. Fish. Aquat. Sci. **64**(2): 375–385. doi:10.1139/f07-003.

Omernik, J.M. 1987. Ecoregions of the Conterminous United States. Ann. Assoc. Am. Geogr. **77**: 118–125. doi:10.1111/j.1467-8306.1987.tb00149.x.

Omi, P.N., Wensel, L.C., and Murphy, J.L. 1979. An application of multivariate statistics to land-use planning: classifying land units into homogeneous zones. For. Sci. **25**(3): 399–414.

Poole, G.C., Dunham, J.B., Keenan, D.M., Sauter, S.T., McCullough, D.A., Mebane, C., Lockwood, J.C., Essig, D.A., Hicks, M.P., Sturdevant, D.J., Materna, E.J., Spalding, S.A., Risely, J., and Deppman, M. 2004. The case for regime-based water quality standards. Bioscience, **54**: 155–161. doi:10.1641/0006-3568(2004)054[0155:TCFRWQ]2.0.CO;2.

Prakash, S., Atkinson, J.F., and Green, M.L. 2007. A semi-Lagrangian study of circulation and transport in Lake Ontario. J. Gt. Lakes Res. **33**: 774–790. doi:10.3394/0380-1330(2007)33[774:ASSOCA]2.0.CO;2.

Randall, R.G., Minns, C.K., Cairns, V.W., and Moore, J.E. 1996. The relationship between an index of fish production and submerged macrophytes and other habitat variables at three littoral areas in the Great Lakes. Can. J. Fish. Aquat. Sci. **53**(S1): 35–44. doi:10.1139/f95-271.

Randall, R.G., Minns, C.K., Cairns, V.W., Moore, J.E., and Valere, B. 1998. Habitat predictors of fish species occurrence and abundance in nearshore areas of Severn Sound. Can. MS Rep. Fish. Aquat. Sci. 2440.

Rao, Y.R., and Schwab, D.J. 2007. Transport and mixing between the coastal and offshore waters in the Great Lakes: a review. J. Gt. Lakes Res. **33**: 202–218. doi:10.3394/0380-1330(2007)33[202:TAMBTC]2.0.CO;2.

Rawson, D.S. 1950. Morphometry as a dominant factor in the productivity of large lakes. Verh. Int. Ver. Limnol. **12**: 164–175. doi:10.1080/03680770.1950.11895282.

Riseng, C.M., Wiley, M.J., Stevenson, R.J., Zorn, T.G., and Seelbach, P.W. 2006. Comparison of coarse versus fine scale sampling on statistical modeling of landscape effects and assessment of fish assemblages of the Muskegon River, Michigan. Am. Fish. Sci. Soc. **48**: 513–533.

Rohweder, J., Rogala, J.T., Johnson, B.L., Anderson, D., Clark, S., Chamberlin, F., Potter, D., and Runyon, K. 2012. Application of wind fetch and wave models for habitat rehabilitation and enhancement projects, 2012 update. Contract report for US Army Corps of Engineers' Upper Mississippi River Restoration, Environmental Management Program.

Rowe, J.S. 1991. Forests as landscape ecosystems: Implications for their regionalization and classification. Southeastern Forest Experimental Station General Technical Report SE 68. pp. 3–8.

Rowe, J.S., and Sheard, J.W. 1981. Ecological land classification: a survey approach. Environ. Manage. **5**: 451–464. doi:10.1007/BF01866822.

Rucinski, D.K., Beletsky, D., DePinto, J.V., Schwab, D.J., and Scavia, D. 2010. A simple 1-dimensional, climate based dissolved oxygen model for the central basin of Lake Erie. J. Gt. Lakes Res. **36**: 465–476. doi:10.1016/j.jglr.2010.06.002.

Rutherford, E., and Geddes, C. 2007. Ecological classification of nearshore and open-water fish habitats in the Great Lakes. Institute for Fisheries Research, University of Michigan School of Natural Resources and Environment, Ann Arbor, Mich.

Sayre, R., Dangermond, J., Frye, C., Vaughan, R., Aniello, P., Breyer, S., Cribbs, D., Hopkins, D., Nauman, R., Derrenbacher, W., Wright, D., Brown Convis, C., Smith, J., Benson, L., Paco VanSistine, D., Warner, H., Cress, J., Danielson, J., Hamann, S., Cecere, T., Reddy, A., Burton, D., Grosse, A., True, D., Metzger, M., Hartmann, J., Moosdorf, N., Dürr, H., Paganini, M., DeFourny, P., Arino, O., Maynard, S., Anderson, M., and Comer, P. 2014. A new map of global ecological land units — an ecophysiographic stratification approach. Association of American Geographers. Washington, D.C.

Scharold, J., Corry, T.D., Yurista, P.M., and Kelly, J.R. 2015. Benthic macroinvertebrate assemblages in the US nearshore zone of Lake Erie, 2009: Status and linkages to landscape-derived stressors. J. Gt. Lakes Res. **41**: 338–347. doi:10.1016/j.jglr.2015.03.020.

Schwab, D.J., Beletsky, D., DePinto, J., and Dolan, D.M. 2009. A hydrodynamic approach to modeling phosphorus distribution in Lake Erie. J Gt. Lakes Res. **35**: 50–60. doi:10.1016/j.jglr.2008.09.003.

Seelbach, P.W., and Wiley, M.J. 2005. Landscape-based modeling as the basis for a prototype information system for ecological assessment of Lake Michigan tributaries. *In* State of Lake Michigan: ecology, health, and management. *Edited by* T. Edsall and M. Munawar. Ecovision World Monograph Series. Aquatic Ecosystem Health and Management Society, New Delhi, India. pp. 559–581

Seelbach, P.W., Wiley, M.J., Baker, M.E., and Wehrly, K.E. 2006. Initial classification of river valley segments across Michigan's Lower Peninsula. Am. Fish. Sci. Soc. **48**: 25–48.

Sheng, J., and Rao, Y.R. 2006. Circulation and thermal structure in Lake Huron and Georgian Bay: application of a nested-grid hydrodynamic model. Cont. Shelf Res. **26**: 1496–1518. doi:10.1016/j.csr.2006.01.019.

Sierszen, M.E., Hrabik, T.R., Stockwell, J.D., Cotter, A.M., Hoffman, J.C., and Yule, D.L. 2014. Depth gradients in food-web processes linking habitats in large lakes: Lake Superior as an exemplar ecosystem. Freshw. Biol. **59**: 2122–2136. doi:10.1111/fwb.12415.

Soranno, P.A., Cheruvelil, K.S., Webster, K.E., Bremigan, M.T., Wagner, T., and Stow, C.A. 2010. Using landscape limnology to classify freshwater ecosystems for multi-ecosystem management and conservation. Bioscience, **60**: 440–454. doi:10.1525/bio.2010.60.6.8.

Sowa, S.P., Annis, G., Morey, M.E., and Diamond, D.D. 2007. A GAP analysis and comprehensive conservation strategy for riverine ecosystems of Missouri. Ecol. Monogr. **77**: 301–334. doi:10.1890/06-1253.1.

Stevens, D.L., and Olsen, A.R. 2004. Spatially balanced sampling of natural resources. J. Am. Stat. Assoc. **99**: 262–278. doi:10.1198/016214504000000250.

ter Braak, C.J.F., and Smilauer, P. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca, New York.

USACE. 1985. Ordinary high water mark and low water datum [online]. Available from http://www.lre.usace.army.mil/Missions/Great-Lakes-Information/Links/Ordinary-High-Water-Mark-and-Low-Water-Datum/. US Army Corps of Engineers.

USDA. 1961. Land capability classification. USDA Soil Conservation Service Agriculture Handbook No. 210. United States Department of Agriculture, Washington, D.C.

Venturelli, P.A., Lester, N.P., Marshall, T.R., and Shuter, B.J. 2010. Consistent patterns of maturity and density-dependent growth among populations of walleye (*Sander vitreus*): application of the growing degree-day metric. Can. J. Fish. Aquat. Sci. **67**(7): 1057–1067. doi:10.1139/F10-041.

Verhamme, E.M., Redder, T.M., Schlea, D.A., Grush, J., Bratton, J.F., and DePinto, J.V. 2016. Development of the Western Lake Erie Ecosystem Model (WLEEM): Application to connect phosphorus loads to cyanobacteria biomass. J. Gt. Lakes Res. **42**: 1193–1205. doi:10.1016/j.jglr.2016.09.006.

Wang, L., Riseng, C.M., Mason, L., Rutherford, E., Wehrly, K., McKenna, J., Castiglione, C., Johnson, L., Sowa, S., Infante, D., Schaeffer, J., Robertson, M., Gaiot, J., Hollenhorst, T., Ciborowski, J., and Coscarelli, M. 2015. A spatial classification and database for management, research, and policy making: the Great Lakes Aquatic Habitat Framework. J. Gt. Lakes Res. **41**(2): 584–596. doi:10.1016/j.jglr.2015.03.017.

Warren, C.E. 1979. Toward classification and rationale for watershed management and stream protection. US Environmental Protection Agency, Corvallis, Oregon. EPA-600/3-79-059.

Webb, P.W., Cotel, A., and Meadows, L.A. 2008. Waves and eddies: effects on fish behavior and habitat distribution. *In* Fish locomotion: an etho-ecological perspective. *Edited by* P. Domenici and B.G. Kapoor. Science Publishers, Enfield, New Hampshire.

Wehrly, K.E., Breck, J.E., Wang, L., and Szabo-Kraft, L. 2012. A landscape-based classification of fish assemblages in sampled and unsampled lakes. Trans. Am. Fish. Soc. **141**: 414–425. doi:10.1080/00028487.2012.667046.

Wehrly, K.E., Wang, L., Infante, D., Cooper, A., Geddes, C., Stanfield, L., and Rutherford, E. 2013. Landscape change and its influences on aquatic habitat and fisheries in the Great Lakes Basin. *In* Great Lakes Fisheries Policy and Management: A Binational Perspective. 2nd ed. *Edited by* W. Taylor, N. Leonard, and A. Lynch. Michigan State University Press, East Lansing, Mich. pp. 81–103.

Wetzel, R. 2001. Limnology: lake and rivers ecosystems. 3rd ed. Academic Press, San Diego, Calif.

Wichert, G.A., MacKenzie, J.S., and Staples, P. 2004. Aquatic ecosystem classification for the Great Lakes watershed in Ontario [online]. Ontario Ministry of Natural Resources. Peterborough, Ontario. Available from http://nhic.mnr.gov.on.ca/MNR/nhic/reports/AEC_Great_Lakes_Watershed.pdf.

Winthers, E., Fallon, D., Haglund, J., DeMeo, T., Nowacki, G., Tart, D., Ferwerda, M., Robertson, G., Gallegos, A., Rorick, A., Cleland, D.T., and Robbie, W. 2005. Terrestrial Ecological Unit Inventory technical guide. US Department of Agriculture, Forest Service, Washington Office, Ecosystem Management Coordination Staff, Washington, D.C.

Wu, J., and David, J.L. 2002. A spatially explicit hierarchical approach to modeling complex ecosystems: theory and applications. Ecol. Model. **153**: 7–26. doi:10.1016/S0304-3800(01)00499-9.

Yurista, P.M., Kelly, J.R., Miller, S.E., and Van Alstine, J.D. 2012. Water quality and plankton in the United States nearshore waters of Lake Huron. Environ. Manage. **50**: 664–678. doi:10.1007/s00267-012-9902-x. PMID:22824959.

Yurista, P., Kelly, J., Cotter, A., Miller, S., and Van Alstine, J. 2015. Lake Michigan: nearshore monitoring and a nearshore–offshore difference in water quality. J. Gt. Lakes Res. **41**: 111–122. doi:10.1016/j.jglr.2014.12.010.

Yurista, P.M., Kelly, J.R., and Scharold, J.V. 2016. Great Lakes nearshore–offshore: Distinct water quality regions. J. Gt. Lakes Res. **42**: 375–385. doi:10.1016/j.jglr.2015.12.002.

Appendix A

Appendix Tables A1 and A2 appear on the following pages.

Table A1. Key drivers and variables.

Supervariable–variable	Source data set	Data description	Data processing	Type*	Zones: Coastal terrestrial	Coastal aquatic	Nearshore	Offshore
Topobathymetry–Slope								
Elevation	NOAA Topobathymetry	Metres above–below sea level	NA	Cont.	×			
Depth (bathymetry)	NOAA Coastal Services Center	Meters below International Great Lakes Datum (IGLD) 1985	NA	Cont.		×	×	×
Slope	Derived from elevation and bathymetry	Degrees	Calculated slope for each 30 m or 1.8 km pixel		×	×	×	×
Relief	Derived from elevation and bathymetry	Metres	Rescaled from 10 pixel rectangular neighborhood	Cont.	×	×	×	×
Geomorphology								
Substrate type	Compilation from Great Lakes Geographic Information System and Great Lakes Aquatic Habitat Framework (GLAHF)	Clay, mud, hard, sand, bedrock	Compiled and harmonized into three to five categories	Cat.	×	×	×	×
Geoform	GLAHF derived bathymetry (depth and relief)	24 classes	Class description	Cat.		×	×	×
Mechanical energy–hydraulics								
Circulation	NOAA Great Lakes Coastal Forecasting System	2006–2012 hourly ***u***, ***v*** (velocity component vectors)	April–May and July–August: mean 2006–2012	Cont.				×
Waves	USACE Wave Information Studies	1979–2012 all lakes hourly wave height and period	Mean and max. wave height (m) and period (s): mean 2006–2012	Cont.	×	×	×	
Fetch	GLAHF	Wind direction weighted distance	Mean 2006–2012			×	×	
Hydroforms (upwelling)	Derived from NOAA CoastWatch Daily Surface Temp.	1993–2012	No. of upwellings·year^{-1}: mean 2003–2012	Cont.		×	×	×
Seiches	NA		NA					
Water levels	Great Lakes Waterlevel Dashboard		Mean 2003–2012	Cont.	×	×	×	×
Temperature–energy								
Surface water temperature	NOAA CoastWatch Daily Surface Temp.	1993–2012	Mean August temp. (°C): 2003–2012	Cont.		×	×	×
Vertical water temperature	NOAA Great Lakes Coastal Forecasting System	2006–2012	Epilimnetic, metalimnetic, and hypolimnetic temperatures: mean 2006–2012	Cont.			×	×
Stratification	NA		NA				×	×
CDD	Derived from NOAA Great Lakes Coastal Forecasting System	2006–2012	Annual sum of epilimnetic temperature for ice-free days: mean 2006–2012	Cont.		×	×	×
Days of ice	Great Lakes Ice Atlas	1973–2011	Data available for daily percent cover of ice for each pixel above a 50% threshold: mean 2003–2012	Cont.		×	×	×
Spring rate of warming	Derived from NOAA CoastWatch Daily Surface Temp.	1994–2012	For each year, temperature on 1 June minus temperature on 1 March and divided by the duration (93 days): mean 2003–2012	Cont.		×	×	×

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Table A1 (*concluded*).

Supervariable–variable	Source data set	Data description	Data processing	Type*	Zones			
					Coastal terrestrial	Coastal aquatic	Nearshore	Offshore
River hydrology								
Distance from river mouth–shore	Great Lakes Aquatic Gap program; GLAHF		Calculated distance from pixel to nearest river mouth	Cont.		×	×	×
Flow hydrology–stream size (index)	USGS–Infante Lab–Stanfield		From terminal reach	Cat.			×	
River thermal regime	USGS–Michigan State University–Ontario Ministry of Natural Resources and Environment	Four categories	From terminal reach	Cat.			×	
Landscape								
Soils (erosion potential)	USA — Natural Resources Conservation Service (NRCS); Canada — Agriculture and Agri-Food Canada (AAFC)	Calculated susceptibility to erosion		Cont.			×	
Soils (permeability)	USA — NRCS; Canada — AAFC	Drainage (inches·h^{-1}; 1 inch = 2.5 cm)		Cont.			×	
Surficial geology (types)	USGS	16 categories		Cat.			×	
Surficial geology (permeability)	USGS	Drainage capacity		Cont.			×	
Bedrock geology	USGS, Ontario Ministry of Northern Development and Mines	10 categories		Cat.			×	
Modifiers								
Land use–cover	Land Use/Land Cover 2000–2001; USGS National Land Cover Database and Ontario Ministry of Natural Resources and Environment; Ag censu	17 categories, harmonized to seven main categories		Cat.	×	×		
Wetland type–location	Great Lakes Commission; GLAHF	Three categories		Cat.	×	×	×	

*Cont., continuous; Cat., categorical.

Table A2. Areal extent of AEUs by lakes.

		Percentage of lake area (%)				
AEU	Area (km²)	Erie	Huron	Michigan	Ontario	Superior
1111	118.08		0.01			0.13
1112	110.78		0.06			0.09
1113	480.83		0.02			0.57
1121	55.46		0.04			0.04
1122	59.26					0.07
1123	65.02		0.02			0.07
1131	61.25		0.06			0.03
1132	9.11					0.01
1133	134.01					0.16
1211	422.11		0.44	0.17	0.30	0.00
1212	364.16		0.22	0.16	0.31	0.09
1213	1 826.64		1.59	0.61	0.55	0.51
1221	124.07		0.07	0.13	0.03	0.01
1222	186.42		0.03	0.09	0.39	0.05
1223	746.29		0.61	0.50	0.12	0.08
1231	74.37		0.08	0.04		0.01
1232	74.94		0.04	0.05	0.02	0.02
1233	419.36		0.29	0.19		0.17
1311	51.31	0.17			0.02	
1312	243.10	0.73	0.01	0.01	0.19	
1313	1 564.88	4.43	0.44	0.09	0.28	
1321	18.59	0.04			0.03	
1322	95.95	0.12	0.02	0.04	0.14	
1323	1 070.12	1.03	1.23	0.01	0.30	
1332	16.03			0.03		
1333	263.48	0.38	0.13	0.11	0.11	
2111	5.65		0.01			0.00
2112	18.89		0.02			0.01
2113	69.23		0.01			0.07
2121	27.06		0.03			0.01
2122	33.87		0.01			0.03
2123	17.60		0.01			0.01
2131	27.61		0.02			0.02
2132	4.37					0.01
2133	52.19					0.06
2211	244.40		0.25	0.09	0.17	0.01
2212	139.00		0.07	0.09	0.12	0.03
2213	719.24		0.54	0.40	0.37	0.12
2221	109.15		0.05	0.13	0.02	
2222	163.37		0.06	0.12	0.22	0.02
2223	499.60		0.36	0.44	0.06	0.02
2231	81.59		0.06	0.08		0.00
2232	83.71		0.02	0.10	0.02	0.01
2233	254.50		0.20	0.13		0.07
2311	325.24	1.19			0.01	
2312	117.46	0.36	0.00	0.00	0.08	
2313	201.63	0.63	0.01	0.01	0.11	
2321	30.74	0.11			0.01	
2322	121.87	0.10	0.05	0.06	0.14	
2323	848.20	1.58	0.64	0.01	0.20	
2332	8.20			0.01		
2333	168.55	0.26	0.08	0.04	0.12	
3141	8 175.47		5.91	1.45	2.34	4.11
3142	2 941.19		0.82	0.87	1.81	1.95
3143	2 037.36		0.85	0.37	0.21	1.55
3241	13 204.87	2.34	9.12	9.57	8.44	
3242	4 738.06	2.21	2.98	3.25	2.56	
3243	4 574.65	2.44	3.15	2.59	2.82	
3341	4 093.43	8.92	0.08	2.72	0.33	
3342	2 042.07	5.25	0.45	0.51	0.31	
3343	2 790.10	8.02	0.71	0.30	0.17	
4250	5 767.24	21.36				
4260	558.40	2.07				
4350	7 072.24	26.20				
4360	601.99	2.23				
5140	7 416.00		2.49	0.23	1.34	6.75
5150	13 348.96		5.83	6.61	10.07	5.04
5160	9 467.64		10.02	0.10		4.19
5240	5 267.82	0.24	3.59	3.85	4.42	
5250	31 037.11	6.75	20.66	23.95	16.08	
5260	6 627.01	0.82	6.43	3.59	2.62	
6140	3 571.36					4.34
6150	53 805.07		10.23			58.05
6160	11 157.58		3.05			11.36
6240	459.52		0.30	0.49		
6250	30 318.54		4.19	34.26	42.03	
6260	1 519.50		1.24	1.35		